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THE BOTANICAL GAZETTE

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THE UNIVERSITY OF CHICAGO PRESS
CHICAGO, ILLINOIS

THE CAMBRIDGE UNIVERSITY PRESS
LONDON AND EDINBURGH

THE MARUZEN-KABUSHIKI-KAISHA
TOKYO, OSAKA, KYOTO, FUKUOKA, SENDAI

THE MISSION BOOK COMPANY
SHANGHAI

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THE BOTANICAL GAZETTE

EDITOR
JOHN MERLE COULTER

VOLUME LXV

JANUARY–JUNE 1918

WITH ELEVEN PLATES AND ONE HUNDRED SIXTEEN FIGURES

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO, ILLINOIS

Published
January, February, March, April, May, June, 1918

Composed and Printed By
The University of Chicago Press
Chicago, Illinois, U.S.A.

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DATES OF PUBLICATION

No. 1, January 17; No. 2, February 15; No. 3, March 15; No. 4, April 15; No. 5, May 15; No. 6, June 18.

ERRATA

VOL. LXV

P. 27, line 20 from top, for *Thurbeir* read *Thurber*

P. 37, line 8 from top, for polliicis read pollicis

P. 299, line 26 from top, for **2**: read **9**:

P. 312, line 19 from top, for civaricata read divaricata

P. 334, line 7 from bottom, for Larangae read Larranagae

P. 338, line 5 from bottom, omit ovated

P. 424, line 23 from top, for **stellapila** read **stellipila**

P. 443, line 12 from top, for 1895 read 1859

P. 447, line 23 from top, for **eximea** read **eximia**

P. 448, line 8 from bottom, for Chapman, Fl. 421, 1861 read Sargent, nov. comb.

P. 465, line 10 from bottom, for **Sphenosporea** read **Sphenospora**

VOLUME LXV NUMBER 1

BU # 0044920

THE

BOTANICAL GAZETTE

JANUARY 1918

A CONSPECTUS OF MEXICAN, WEST INDIAN, CENTRAL AND SOUTH AMERICAN SPECIES AND VARIETIES OF SALIX

CAMILLO SCHNEIDER

In March 1917, at the request of Professor SARGENT, director of the Arnold Arboretum, I commenced a study of the American willows. A monograph of the genus *Salix* as far as it is represented in America[1] is certainly badly needed, but the attempt to investigate thoroughly the numerous species and forms described since ANDERSSON wrote his review in 1868 will prove a difficult task. It is not without a great deal of hesitation, therefore, that I have undertaken it, and I venture to ask the assistance of every one interested in the study of willows. I have already made a rather extensive investigation of the forms belonging to the PLEIANDRAE group (sect. NIGRAE, TRIANDRAE, PENTANDRAE subsect. LUCIDAE, and BONPLANDIANAE) and to sect. LONGIFOLIAE. At present I am occupied with the species of the sect. ARTICAE,

[1] In regard to the willows of the Old World it may be mentioned that there is a good account of those of Central Europe by O. v. SEEMEN in ASCHERSON and GRAEBENER, Syn. Mitteleurop. Fl. 4:54–350. 1908–9. Of the species of Eastern Asia and of the Himalayas I have given an enumeration in SARGENT, Pl. Wilson. 3:40–179. 1916. The willows of Central and Western Asia and those of Northern Europe and Northern Asia are very imperfectly known. I believe, however, that Rev. S. J. ENANDER, Lillherrdal, Sweden, the foremost living salicologist, is preparing a monograph of the whole genus.

RETUSAE, and RETICULATAE. I shall not deal with the forms of sect. CORDATAE because C. R. BALL, the well known salicologist at Washington, D.C., has already undertaken a monograph of this special group. Should anyone else be interested in a special study of any other section or group of the North American willows I should be very glad to hear from him.

In this article I intend to discuss the willows known from Mexico, Central America, and South America. There are among them many forms which, in my opinion, need a careful study in the field, and which are more or less closely related to forms from the southern parts of the United States. So far as I know, there has never been an attempt to give a critical review of these willows, but it seems to me impossible to determine any Mexican willow without having tried to interpret properly the species already described from that region.

I wish to express my thanks to the gentlemen in charge of the following herbaria for the opportunity to study the material contained in the different collections: Herbarium of the Arnold Arboretum, Gray Herbarium, Herbarium of the Missouri Botanical Garden, Herbarium of the New York Botanical Garden, and the United States National Herbarium at Washington.

The last enumeration of the Mexican willows was given by W. B. HEMSLEY (Botany, Biol. Central. Amer. 3:179–180. 1883), but there is no critical examination of them. Since then several new species have been described by O. v. SEEMEN and by W. W. ROWLEE, which partly, as will be shown in the following notes, are founded on a wrong interpretation of already existing species. Unfortunately, the types of most of those species are in European herbaria, and I have not been able to examine them, especially the types of the species established by MARTENS and GALEOTTI mostly on sterile branches. In consequence of this lack of important material I am not sure that my interpretation is correct in every case. Not only a careful study of the type specimens but also a more careful investigation of most of the species in the field is needed, and it is indeed the main purpose of this paper to draw the attention of all interested in the flora of Mexico and South America to what is still unknown of the willows of those countries.

Clavis specierum

Stamina 3 vel plura

Folia adulta ramulorum sterilium surculorumque utrinque concoloria, viridia, linearia, lineari-lanceolata vel anguste lanceolata (rarius in surculis late lanceolata), utraque pagina stomatibus pl. m. aequinumerosis instructa

Ramuli annotini biennesque pl. m. rubescentes vel purpurascentes; ovaria pedicellique glabri

Fructus perfecte maturi ovoidei, ovoideo-oblongi vel elliptici, apice vix vel tantum breviter attenuati, pedicello brevi iis pleroque 4–5plo breviore glandulam circ. 2–3plo superante suffulti; folia linearia vel lineari-lanceolata (rarius in surculis *S. Humboldtianae* var. *Martianae* late lanceolata), stipulae intus (an semper?) eglandulosae

1. *S. Humboldtiana*

Fructus perfecte maturi ovoideo-lanceolati, apice satis attenuati, pedicello satis variabili glandulam 2–5plo superante suffulti; folia lineari-lanceolata ad late lanceolata; stipulae intus pl. m. glanduliferae

2. *S. nigra*, var. *Lindheimerii*

Ramuli annotini biennesque pl. m. distincte flavescentes vel flavo-cinerei; ovaria fructusque vel pedicelli tantum saepe pilosi; fructus ovoideo- vel anguste elliptico-lanceolati, apice pl. m. attenuati, plerique satis longe pedicellati . . . . . 3. *S. Gooddingii*

Folia adulta ramulorum sterilium surculorumque subtus discoloria, glaucescentia

Ramuli annotini biennesque flavescentes vel flavi; folia superne stomatibus numerosis instructa; petioli satis tenues et longi, quam lamina vix ultra 6plo breviores . . . . . 4. *S. amygdaloides* var. *Wrightii*

Ramuli annotini biennesque rubescentes vel purpurascentes vel tomentelli; folia superne nunquam stomatifera

Fructus satis parvi et crassi, breviter ovoideo-conici, apice vix vel paullo attenuati, 4–5 mm. longi, pedicello satis crasso iis 4–5plo breviore excluso, vel pedicelli (basisque fructuum) pilosi

Ramuli annotini dense tomentosi; folia initio subtus dense villoso-tomentosula; petioli breves, vix ad 8 mm. longi; amenta mascula parva, tenuia, vix ad 3:0.8 cm. magna; fructus conferti circ. 4 mm. longi, basi pedicelloque pilosi . . . . . 5. *S. jaliscana*

Ramuli annotini glabri (hornotini tantum interdum pilosi); folia subtus semper glabra vel cito glabrescentia vel petioli foliorum majorum ultra 10 mm. longi; amenta saepissime serotina, in axillis foliorum adultorum apparentia, vel coetanea, mascula pleraque 4–6 cm. longa; fructus circ. 5 mm. longi, pedicello 4–6plo breviore excluso, glabri . . . . . 6. *S. Bonplandiana*

Fructus 5–9 mm. longi, apice subito vel sensim attenuati vel pedicello gracili tantum duplo breviore instructi

Stipulae in facie intus pl. m. glanduliferae, parvae vel nullae; folia matura superne vivide viridia, nitidula, margine saepissime satis indistincte et adpresse denticulata; fructus vix ultra 6 mm. longi, pedicello subduplo ad 3plo breviore excluso.....7. *S. laevigata*

Stipulae in facie intus tantum pl. m. pilosae vel glabrae, saepe (saltem in surculis) satis magnae; folia matura superne pl. m. sed obscure viridia, margine saepissime argutius glanduloso-serrato-denticulata; fructus 6–10 mm. longi, pedicello pleroque subduplo vel duplo breviore excluso.....8. *S. longipes*

Stamina tantum 2

Folia minima vel parva, pl. m. linearia vel lanceolata, utrinque aequaliter stomatifera, vel flores masculi semper glandulis 2 (ventrali dorsalique[2]) instructi, vel amenta tardiva, ramulos satis longos foliatos terminantia anguste linearia

Amenta brevia, mascula 5–13 mm. longa et circ. 8 mm. crassa, feminea satis pauciflora, fructifera haud ultra 2 : 1 . 2 cm. magna; antherae minimae, globosae vel breviter ellipticae, haud vel paullo longiores quam latae; stigmatum lobi lineares vel lineari-lanceolati.....9. *S. taxifolia*

Amenta longiora vel antherae ellipticae, circ. 1 . 5plo ad 2plo longiores quam latae vel stigmatum lobi breves oblongi

Flores masculini glandulis 2 instructi; ovaria glabra vel pl. m. pilosa, pilis haud micantibus.....10. *S. exigua* var.

Flores masculini glandula tantum ventrali instructi; ovaria densissime sericeo-villosa, pilis micantibus...11. *S. longifolia* var. *angustissima*

Folia majora vel latiora et nunquam superne stomatifera (si folia sunt parva glandula dorsalis in floribus masculis deest et ovaria longe pedicellata sunt)

Amenta in axillis foliorum adultorum apparentia, vix ultra 2 cm. longa, vel flores masculi (in *S. Schaffnerii* ignoti) etiam glandula dorsali parva praediti; stigmata parva; ovaria pedicellique glabri vel sparse pilosi

Ramuli hornotini annotinique tomentosi; folia subtus (saltem in costa) pl. m. tomentella

Gemmae foliiferae apice pl. m. rostratae, ad 8 mm. longae, glabrae, vel apice sparse pilosae; pedicelli ovariorum glandula 2–2 . 5plo longiores, bracteam haud superantes.....12. *S. Hartwegii*

Gemmae foliiferae tantum acutae, vix ultra 6 mm. longae, pl. m. villoso-tomentellae; pedicelli ovariorum graciles, glandula 4–5plo longiores, bracteam pl. m. superantes.....14. *S. Schaffnerii*

Ramuli semper glabri; folia glabra.....13. *S. mexicana*

Amenta praecocia vel coetanea; flores masculi tantum glandula ventrali instructi

Inflorescentiae satis magnae ultra 2 . 5 cm. longae; folia etiam mediocra ultra 2 . 5 cm. longa.

[2] With regard to the nomenclature of these glands see my note in SARGENT, Pl. Wils. 3:94. 1916.

Ovaria glabra, tantum pedicelli interdum pilosi; stigmata brevia; filamenta glabra, libera vel $\frac{1}{6}$–$\frac{1}{3}$ coalita

Folia lanceolata, oblanceolata vel anguste elliptica, saepissime ultra 3plo longiora quam lata; amenta mascula satis anguste cylindrica, vix plus quam 12 mm. crassa; filamenta basi pl. m. coalita; stigmata minima, stylis pluriplo breviora; bracteae pl. m. obovatae, apice valde obtusae vel truncatae. . . . . 15. *S. lasiolepis*

Folia elliptica vel late elliptico-lanceolata, vix ultra 3plo longiora quam lata; amenta mascula crasse cylindrica, 1.5–2 cm. crassa; filamenta libera; bracteae oblongae, pl. m. acutae; stigmata mediocra stylis fere aequilonga. . . . . 16. *S. Rowleei*

Ovaria (in *S. oxylepide* ignota) villosa, stigmata lanceolata; filamenta basi pl. m. pilosa, libera

Bracteae anguste lanceolatae, apice distincte acutae vel breviter acuminatae . . . . . 17. *S. oxylepis*

Bracteae oblongae, apice pl. m. obtusae vel subtruncatae, rarius acutiusculae . . . . . 18. *S. paradoxa*

Inflorescentiae parvae, ut videtur vix ad 1 cm. longae; folia visa nondum matura tantum ad 1.8 cm. longa (vide etiam *S. Endlichii*, in nota post *S. canam*) . . . . . 19. *S. cana*

Enumeratio sectionum specierumque

Sect. I. NIGRAE Loudon, Arb. Frut. Brit. **3**:1529. 1838; SCHNEIDER, Ill. Handb. Laubh. **1**:32. 1904.—Sect. AMYGDALINAE Ball in Coult. and Nels., New Man. Rocky Mt. Bot. 129. 1909, quoad *S. nigra*.

The species belonging to this well distinguished section are *S. nigra* Muhl., *S. Humboldtiana* Willd., and *S. Gooddingii* Ball. ANDERSSON (K. Svenska Vet. Akad. Handl. **6**:15. 1867; and DC. Prodr. **16**^{2}:199. 1868) refers *S. Humboldtiana* to his section AUSTRO-AMERICANAE vel HUMBOLDTIANAE, but he also includes *S. Bonplandiana* Kth., which certainly does not belong to the same group. *S. nigra* is included by ANDERSSON and other authors in sect. AMYGDALINAE (vel TRIANDRAE) together with *S. amygdaloides* And. In my opinion, *S. nigra* is much more closely related to *S. Humboldtiana* than to *S. amygdaloides* or any other species of sect. AMYGDALINAE. The species of sect. NIGRAE are exclusively American, and show no very close relationship to any other group of American willows or any section of those of the Old World. H. GÄRTNER (Vergl. Blattanatomie Gatt. Salix, Diss. Göttingen, 1907,

p. 22) apparently did not examine a true *nigra* because he does not mention the stomata in the upper surface of the leaf, but says "unterseits Stomaten und Wachsanflug." *S. nigra*, like *S. Humboldtiana*, possesses however "beiderseits Kutikularfalten und eine gleichgrosse Anzahl von Stomaten."

1. S. HUMBOLDTIANA Willd., Sp. Pl. **4**:657. 1805; Kunth in Humb. and Bonpl., Nov. Gen. Pl. **2**:18, *pls. 99, 100.* 1817; Syn. Pl. Aequin. **1**:364. 1822; Gay, Hist. Chile Bot. **5**:384. 1849; Leybold in Martius, Fl. Bras. **4**[1]:227. *pl. 71*, 1855; de la Sagra, Fl. Cubana **3**:232. 1853; Grisebach, Fl. Brit. W. Ind. Isl. 113. 1864; Philippi, Cat. Pl. Vasc. Chile, 267. 1881; Hieron., Pl. Diaph. Fl. Argent. 271. 1882; Fawcett, Prov. List Flow. Pl. Jamaica 37. 1893; Duss in Ann. Inst. Col. Marseille **3**:107 (Fl. Phan. Antill. Franç.). 1897; Macloskie in Princeton Univ. Exp. Patag. **8**[1]: Bot. 325 (Fl. Patag.) 1903–6; *S. magellanica* Poir. in Lam. Encycl. Suppl. **5**:66. 1817; *S. falcata* Kunth in Humb. and Bonpl., Nov. Gen. Pl. **2**:19. 1817, non Pursh; *S. Humboldtiana*, ***S. falcata* And. in K. Sv. Vet.-Akad. Handl. **6**:17 (Mon. Salic.). 1867; *S. Humboldtiana* β *falcata* And. in DC. Prodr. **16**[2]:199. 1868; *S. chilensis* Morong and Britton in Ann. N.Y. Acad. Sci. **7**:231 (Enum. Pl. Morong Paraguay). 1892, non Molina;[3] Seemen in Urban Symb. Antill. (Fl. Ind. Occ.) **4**:193. 1905; Fawcett and Rendle, Fl. Jamaica **3**:30. 1914.

TYPE LOCALITY.—"Peru, prope Loxam" (leg. *Humboldt* and *Bonpland*); this is Loja in southern Ecuador.

RANGE.—According to MORONG this willow "grows from the Amazon to Patagonia on both sides of the Andes." It is difficult to say where it is really spontaneous, because it has been widely distributed by cultivation. Although

[3] *S. chilensis* Molina, SAGGIO Storia Nat. Chili 169. 1782, is in my opinion an obscure plant. The author's quotation runs: "*Salix* fol. integerrimis glabris lanceolatis acuminatis," and in the Italian text he says: "Il Salce, *Salix chilensis* . . . . non differisce dall' Europeo, che nelle foglie, le quali sono intiere, sottili, e di un verde giahligno: questo albero produce una gran quantita di manna tutti gli anni. . . . ." Neither has *S. Humboldtiana* entire leaves, nor can I find any record of a willow producing "manna." The name *S. chilensis* seems to be accepted for our willow only because there is no other willow in Chile except the cultivated *S. babylonica* L. which had not yet been introduced at MOLINA'S time. I strongly suspect that MOLINA'S plant is no *Salix* at all. It is not mentioned by REICHE in his Productos Vegetales de Chile, 1901, nor in ENGLER and DRUDE, Veget. der Erde VIII (Grundzüge Pflanzenwelt Chile). 1907.

I have seen specimens from Argentine, Chile, Uruguay, Paraguay, Bolivia, Peru, Colombia, and southern Brazil I do not have a correct understanding of the wild habitat of this species, most of the material before me coming, apparently, from cultivated plants. I suppose *S. Humboldtiana* inhabits river valleys in the cold and temperate region from the Straits of Magellan to southern Brazil in the east and Ecuador in the west. Farther north, in Colombia and on the West Indian Islands, it seems to be only planted, but may occur sometimes escaped from cultivation. In Central America and in Mexico it is represented by var. *stipulacea*.

SPECIMENS EXAMINED.—I have not seen the type, which seems to be preserved in WILLDENOW's herbarium at Berlin, and I do not deem it necessary to enumerate here all the specimens I have seen because, as I have already said, most of them seem to be taken from cultivated plants.[4]

S. Humboldtiana is apparently a well marked species, and I deal with its relationship to *S. nigra* under var. *stipulacea*.

1b. S. HUMBOLDTIANA, var. **stipulacea** Schn., comb. nov.—*S. Houstoniana* Pursh, Fl. Am. Sept. **2**:614. 1814. quoad specim. Houstonianum ex Herb. Banks; *S. stipulacea* Mart. and Galeotti in Bull. Ac. R. Brux. **10**[1]:343 (Enum. Pl. Gal. Mex. 3) 1843; *S. Humboldtiana* ****S. oxyphylla* And. in K. Sv. Vet.-Akad. Handl. **6**:17 (Mon. Salic.). 1867, pro. parte; *S. Humboldtiana* γ *oxyphylla* And. in DC. Prodr. **16**[2]:199. 1868, pro parte; Bebb apud Smith Enum. Pl. Guat. part **2**:71. 1891; part **3**:76. 1893; *S. Humboldtiana* Mart. and Gal. in Bull. l. c. non Willd.; Hemsl. in Biol. Centr. Am. Bot. **3**:179. 1883, pro parte.

A typo praecipue recedit foliis non distincte linearibus sed pl. m. lineari-lanceolatis fere a basi ad ápicem sensim attenuatis apice plerisque distinctius caudato-acuminatis et basi magis cuneato-attenuatis, stipulis saltem ramulorum validorum distinctius evolutis.

TYPE LOCALITY.—State Hidalgo, "au bord du Rio Grande de Mextitlan [Metztitlan] près du district de Real del Monte" (coll. *H. Galeotti*, no. 75, ex Martens and Galeotti).

RANGE.—This variety seems to reach its most northern point in Hidalgo, from where its range extends southward into Guatemala, Salvador, and Costa Rica, but I am not sure whether it is really spontaneous in the last two countries. It is probably also planted, together with the type, on the West Indian Islands.

[4] An enumeration of all the specimens I have examined will be given in the final publication of my studies on American willows.

SPECIMENS EXAMINED.—I have seen what I believe may be specimens from wild plants from the following states of Mexico: Hidalgo, Colima, Vera Cruz, Oaxaca, Tabasco, and Chiapas, and from the following Departments of Guatemala: Alta Verapaz, Izabal, Jalapa, Guatemala, Sololá, Amatitlan, and Zacatepequez.

The vàr. *stipulacea* is certainly very closely related to the typical *S. Humboldtiana*, but from the material before me I judge it to be a good geographical form which in some respect approaches *S. nigra*. The main difference between *S. Humboldtiana* and *S. nigra*, in my opinion, is the shape of the mature fruits which are ovoid-elliptical with a rather blunt apex in the first; while those of *S. nigra* and its varieties are more distinctly elongated and pointed at the apex, with mostly comparatively longer pedicels. Regarding the shape of the fruit, var. *stipulacea* has to be referred to *S. Humboldtiana;* the leaves, however, resemble more those of *S. nigra* var. *Lindheimerii*. There are indeed several forms in Hidalgo (namely, the specimens of C. S. PRINGLE from Tula, March 23, 1906) that need further observation in the field. They possess the glandular stipules of var. *Lindheimerii* and the fruits of var. *stipulacea*. In the state of Hidalgo the most southern forms of *S. nigra* seem to meet the most northern ones of *S. Humboldtiana*.

As to the nomenclature of the variety, the following may be said. Most of the authors used to refer it to *S. oxyphylla* Kth. in Humb. and Bonpl., Nov. Gen. Pl. **2**:19. 1817; Syn. Pl. Aequ. **1**:365. 1822, the type of which was collected by *Humboldt* and *Bonpland* "prope Chilpantzingo" (Chilpanzingo, in the state of Guerrero). Not having been able to compare a type specimen, nor having seen any specimen from near the type locality, I refrain from using the name *oxyphylla*, because in the description KUNTH makes the following statement: "semina minuta, oblonga, lanata; stipite dimidiam vix lineam longo, pubescente." The whole seed being hardly half a line long and having no "stipes," the statement seems to indicate a pubescent pedicel of the ovary, but I have not met with such a form. I regard *S. oxyphylla* as an uncertain name, therefore, and I accept the name *stipulacea* given by MARTENS and GALEOTTI to a form that differs from *S. Humboldtiana* by its persistent stipules and its more sharply acuminate leaves.

1c. S. HUMBOLDTIANA, var. MARTIANA And. in DC. Prodr. **16**^{2}:199. 1868.—*S. Martiana* Leybold in Martius, Fl. Bras. **4**^{1}:228. *pl. 72*. 1855; in Walp. Ann. Bot. **5**:757. 1858; Huber in Bull. Herb. Boiss. II. **6**:253. 1906, in adnot.; *S. Humboldtiana* **S. Martiana* And. in K. Sv. Vet.–Akad. Handl. **6**:18 (Mon. Salic.). 1867.

Varietas porro observanda a typo praecipue differre videtur floribus femineis glandula etiam dorsali (an semper?) instructis, fructibus ellipticis utrinque pl. m. obtusis paullo majoribus.

TYPE LOCALITY.—"In omni ripa et in insulis sabulosis flum. Amazonum a Gurupà (prov. Para in Brasilia) at Peruviam usque frequens."

RANGE.—This variety seems to be confined to the territories of the Amazon and Solimoes River in Brazil, and probably in the adjacent part of Colombia.

SPECIMENS EXAMINED.—Brazil; Prov. Para, "in vicinibus Santarem," July 1850, *R. S. Spruce* (fr.; G.);[5] Lower Amazons, Prainha, marshy beach, November 18, 1873, *I. W. H. Traill* (no. 717, fr.; G.)—Colombia (?), without locality (Herb. Lehmannianum, B.T. 1261, f., fr.).

The material before me is much too scanty to judge the value of this variety. The main characters by which it may be separated from typical *S. Humboldtiana* seem to be the presence of a dorsal gland in the pistillate flowers and the more elliptical shape of the somewhat larger capsules. In SPRUCE's specimen two of the otherwise normal leaves are broadly lanceolate, the larger being about 21 mm. wide. LEYBOLD gives as another distinguishing character the hairy pedicels which, however, are glabrous on the specimens before me. This form needs further investigation.

2. S. NIGRA Marsh., var. **Lindheimerii** Schn., nov. var.—*S. Humboldtiana*, γ *oxyphylla* And. in DC., l. c. 199, quoad specim. Berlandierii no. 2317, 3026; *S. nigra* Mackensen, Trees Shrubs San Antonio 14. 1909, non Marsh.; *S. Wrightii* Sargent, Trees and Shrubs **2**:215. 1913, quoad specimina texana, non And.; *S. Humboldtiana* Blankinship in Rep. Miss. Bot. Gard. **18**:194. 1907, non Willd.

Arbor ad 15–20 m. alta, trunco ad 0.75 m. crasso, cortice cinereo-brunnescente rugoso; ramuli novelli pl. m. pilosi vel villosuli, cito glabrescentes vel glabri, hornotini olivacei vel flavo-brunnei, annotini brunnescentes, dein cinereo-brunnei vel cinereo-fusci, satis graciles tenuesque, teretiusculi; gemmae ovatae, acutiusculae, petiolis subtriplo breviores, apice divaricatae. Folia adulta satis firma, linearia, lineari-lanceolata vel majora anguste lanceolata, ramulorum principalium steriliumque[6] (inferioribus

[5] I am using the following abbreviations: G., Gray Herbarium; M., Herbarium Missouri Botanical Garden; N., Herbarium New York Botanical Garden; W., U.S. Nat. Herbarium, Washington, D.C. If there is no indication of a herbarium the specimens are in A., the herbarium of the Arnold Arboretum (and mostly also in the other herbaria); also, m., male specimen; f., female specimen in anthesis; fr., fruiting specimen (im. fr. means with immature fruits); st., sterile specimen.

[6] I distinguish 3 different kinds of leaves: (1) those of the ends of main and sterile branchlets and of vigorous shoots (offshoots and suckers), which usually represent the typical mature leaves toward the end of the season; (2) those of the lower parts of these parts, representing the leaves of the first season's growth which are

exceptis) basi sensim in petiolum attenuata, ab infra medium ad apicem sensim acuminata, apice satis longe caudata, saepe falcata, 7:0.3 vel 8:0.6 ad 12:0.7 vel 15:1.2 cm. magna, inferiora saepe lineari-elliptica, utrinque obtusiora vel obtusa, ramulorum fertilium (pedunculorum) variabilia, saepe elliptico-linearia vel anguste elliptica, utrinque acuta vel obtusiora, 2:0.3 ad 6–7:0.7–0.9 cm. magna, superne tantum valde initio sparse puberula et citissime glabrescentia, vivide viridia, ut in *Humboldtiana* reticulata et nervo intra-marginali percursa, subtus concoloria, initio ut superne vel saepe paullo magis pilosa, dein glaberrima, eodem modo reticulata, margine satis dense aequaliter glanduloso-serrato-denticulata vel in foliis inferioribus ramulorum fertilium indistinctius dentata vel interdum subintegerrima. Petioli quam in *S. nigra* pl. m. longiores, latitudinem maximam laminae plerique superantes, 2–10 mm. longi. Stipulae satis rariter distincte evolutae, iis formae typicae similes sed intus in facie pl. m. glanduliferae, vix ultra 8 mm. longae. Amenta fere ut in forma typica sed saepissime magis laxiflora, mascula ad 7:0.8 cm. magna; stamina 3–7, filamentis ad medium vel paullo ultra dense villosis; bracteae ovatae vel ovato-oblongae, pl. m. acutae, rarius obtusae, utrinque villosulae vel extus ultra medium ad apicem glabrescentes; glandulae 2, dorsalis pl. m. 3-partita (digitata); amenta feminea fructifera 4–7:1.3 cm. magna (pedunculis foliatis interdum ad 4 cm. longis exclusis), pl. m. laxiflora; bracteae ovato-oblongae, pl. m. acutae, interdum ad apicem parce denticulatae, ut in floribus masculis villosae; ovaria stigmataque ut in *S. nigra* typica; glandula 1, ventralis, pl. m. ovata-rectangularis, apice truncata, pedicello juvenili duplo brevior; fructus maturi (5–)6–7 mm.

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mostly of a different shape, and often more resemble those of the fertile branchlets; and (3) those of the fertile branchlets, that is, of the peduncles or the branchlets terminated by the catkins. It seems to me very helpful to keep apart those 3 different kinds of leaves, of which as a rule only one or two are represented in a specimen. Therefore, every collector of willows should try to get, at different times of the year, if possible from the same plant and of both sexes, the following parts: (1) branchlets with young flowers; (2) branchlets with ripe fruits collected when the first capsules begin to open; (3) mature leaves collected toward the end of the season (end of August to end of September, except in subtropical climates); (4) parts of offshoots with mature and young leaves; (5) leafless branchlets in winter with good buds, and pieces of bark.

longi, iis formae typicae similes sed basi pl. m. subito attenuati, pedicellis satis tenuibus 2–3plo brevioribus glandulam siccam 4–6plo superantibus suffulti.

TYPE LOCALITY.—Texas, Comal County, on the Guadalupe River (leg. *Lindheimer*, no. 415).

RANGE.—Eastern and southeastern Texas (perhaps also in southern Oklahoma), from about 34° N. lat. and between 100 and 95° W. long. southward into Mexico to southeastern Coahuila, Nuevo Leon, and to Tamaulipas (and probably also Hidalgo).

SPECIMENS EXAMINED.—Texas: Comal County, New Braunfels, on the Guadalupe and other rivers, 1850, *F. Lindheimer* (no. 415, m., f., fr., type!; G., M.; in the Gray herbarium named by ANDERSSON himself *S. nigra* var. *angustifolia;* it is the same as no. 1189 distributed by the Mo. Bot. Gard. as *S. Humboldtiana*).—Mexico: State of Tamaulipas: Matamoros, March 1836, *J. J. Berlandier* (no. 3026, fr.; sub nomine inedit. "S. viridis"; G., M.); without exact locality (perhaps from Texas), *J. J. Berlandier* (no. 854, st.; M.; no. 887, fr.; G., M.; no. 2274, st.; G., M.; no. 2317, fr.; G., M.); vicinity of Victoria, alt. about 320 m., February 1—April 9, 1907, *E. Palmer* (no. 134, m.; M., W.).—State of Nuevo Leon: Monterey, May 1891, *C. K. Dodge* (m., fr.; W.; forma porro observanda); same locality, common, March 19–20, 1900, *C. S. Sargent* (m., f.; "large tree"); same locality, March 18–19, 1900, *W. M. Canby* (nos. 231, f., 232, m.; G., W.); same locality, March 18, 1900, *W. Trelease* (no. 131, f.; M.).—State of Coahuila:[7] Ciudad Porfirio Diaz, April 8, 1900, *W. Trelease* (no. 133; M.; fructibus juvenilibus ad *S. Humboldtianam* spectans); Saltillo, April 15–30, 1898, *E. Palmer* (no. 27, m.; "tree of 30 ft. or more high, rather rough bark, not seen over 1 ft. in diam., about watercourses and cultivated places, indicating artificial planting"); mts. 6 miles east of Saltillo, April 1888, *E. Palmer* (no. 1286, m.; G., W.); Pueblo near Saltillo, March 18, 1847, *J. Gregg* (no. 296, m.; M.); San Bernardo or "Green Spring," April 8. 1847, *J. Gregg* (no. 479, m., fr.; M.).

This willow, which has hitherto been regarded either as *S. nigra* or *S. Humboldtiana*, seems to me to represent the most southern form of *S. nigra*. It is not always easy to separate it from typical *nigra* from northern Texas, but the leaves are usually narrower or at least more attenuated at the base, with a comparatively much longer petiole. The young branchlets and the petioles are glabrous or become so very soon, while those of *S. nigra* and its southeastern var. *altissima* Sarg. are, for some time at least, more or less distinctly puberulous or villose. Moreover, the stipules of var. *Lindheimerii* bear always some

[7] There is a specimen collected by C. G. PRINGLE, Jimulco, by streams, alt. 1300 m., October 10, 1905 (no. 10086½, fr.; G.; "a medium sized tree"), bearing only short dense aments (1–2.5:1 cm.), with small, linear-lanceolate, almost entire leaves (about 2–3:0.4–0.5 cm.) on the short peduncles which, I believe, has to be referred to var. *Lindheimerii*.

minute yellowish glands upon the inner surface, which are absent in the typical black willow and var. *altissima*. The fruits of var. *Lindheimerii* are somewhat larger (6–7 mm. long) than those of the typical form (4–5 mm.). On the other hand, the Mexican specimens are often very similar to those of *S. Humboldtiana*, var. *stipulacea;* from this var. *Lindheimerii* seems to be best distinguished by its looser fruiting catkins, its more elongated fruits with longer and thinner pedicels, its leaves being more distinctly attenuated at the base, and by its comparatively longer petioles.

There are the following specimens from western Mexico which may represent a distinct form of var. *Lindheimerii* or a new variety of *S. nigra*. From a geographical point of view one might expect those plants to be a form of *S. Gooddingii*, but the color of the older branchlets, although being not quite so reddish brown as in var. *Lindheimerii*, is much more like it than *S. Gooddingii*. I do not dare to propose a new variety, but I want to draw the attention of collectors to it in the hope that they may be able to procure good flowering material, ripe fruits, and mature leaves.

Mexico: State of Sinaloa, vicinity of Guadalupe, April 18, 1910, *J. N. Rose*, *P. C. Standley*, and *P. G. Russell* (no. 14780, st.; W.; folia lineari-lanceolata iis var. *Lindheimerii* simillima, ad 13 cm. longa et 9 mm. lata, basi valde acuta, petiolis gracilibus fere ad 1 cm. longis); vicinity of Villa Union, moist field, April 2, 1910, same coll. (no. 13955, m., N., W.; folia ut in praecedente, amenta parva, vix 2.5:0.6 cm. magna; bracteae versus apicem amenti acuminatae, basim versus obtusiores; pedunculi vix 1 cm. longi, folia plura linearia ad 3 cm. longa gerentes); vicinity of Culiacan, April 21, 1910, same coll. (no. 14893, f., st.; N., W.; folia maxima ad 13:1.4 cm. magna, petiolis ad 15 mm. longis; flores ut in var. *Lindheimerii;* fructus immaturi circ. 5 mm. longi pedicello duplo breviore).—Terr. Tepic, Santiago, February 1895, *F. H. Lamb* (no. 581, f.; G., M., N.; a var. *Lindheimerii* praecipue differt bracteis florum juvenilium acuminatis et pubescentia distinctiore ramulorum novellorum; amenta valde laxiflora, ad 8 cm. longa, fructibus nondum maturis); vicinity of Acaponeta, April 11, 1910, *Rose*, *Standley*, and *Russell* (no. 14362, st.; N., W.; ramuli hornotini flavescentes, ceterum ut in var. *Lindheimerii*).

3. S. GOODDINGII Ball in BOT. GAZ. **40**:376, *pl. 12, figs. 1, 2.* 1905. —*S. nigra* Bebb in Watson, Bot. Calif. **2**:83. 1879, non Marsh.; Jepson, Fl. Cal. **2**:339. 1909; Parish, Cat. Pl. Salton Sink 3. 1913 (reprinted from "The Salton Sink," Publ. no. 93, Carnegie Inst. Wash.); Wooton and Standley in Contrib. U.S. Nat. Herb. **19**:161 (Fl. N.Mex.). 1915; *S. nigra*, var. *vallicola* Dudley apud Abrams, Fl. Los Angeles 100. 1904; Suppl. Ed. 100. 1911; *S. vallicola* Britt., N.Am. Trees 184. *fig. 141.* 1908; *S. Wrightii* Woot. and Standl. in Contrib. l. c. 160. 1915, non And.

TYPE LOCALITY.—Southeastern Nevada, Clark County, Muddy Creek (coll. *Goodding*, no. 689, f.; forma satis abnormalis ab insectis infecta).

RANGE.—California, southeastern Nevada, Arizona, southwestern New Mexico (probably also east of the Rio Grande and even in southern Colorado), and northern Mexico (Chihuahua, Sonora, northern Sinaloa, northern Lower California).

SPECIMENS EXAMINED (from Mexico).—Lower California: Gardner's Laguna, April 21, 1894, *L. Schoenfeldt* (no. 2895, st.; W.); Seven Wells, on the Salton River, April 8, 1894, *E. A. Mearns* (no. 2869, m.); along Hardy River, April 3, 1905, *D. McDougal* (no. 100, f.; N.; "small tree").—State of Sonora: Sonora shore of Colorado River near International Boundary, March 27, 1905, *D. McDougal* (no. 90, m.; N.; "tree 30–40 ft."); Colonia Diaz, May 29, 1894, *E. A. Mearns* (no. 2840, m.; G., M., N., W.); La Chumata, alt. 1330 m., May 29, 1905, *W. W. Brown* (st.); vicinity of Magdalena, April 25, 1910, *J. N. Rose*, *P. C. Standley*, and *P. G. Russell* (no. 15113, fr.; W.); vicinity of Hermosillo, bed of Rio de Sonora, March 5, 1910, same coll. (no. 12391, fr.; N., W.; "5 ft. or less"; forma porro observanda pedicellis fructuum subbrevioribus); along irrigating ditches, March 7, 1910, same coll. (no. 12501, m., f.; W.; forma porro observanda); vicinity of Navojoa, March 21, 1910, same coll. (no. 13156, fr.; N., W.; ut praecedens).—State of Chihuahua: along the Rio Grande near Ciudad Juarez, 1911, *E. Stearns* (fr.; N.; mixed with male *S. exigua*, var. *stenophylla*); vicinity of Chihuahua, alt. about 1300 m., April 8–27, 1908, *E. Palmer* (nos. 41, f., 42, m.; N.; forma porro observanda); Santa Eulalia Mts., April 1885 (3 ?), *Wilkinson* (m.; W.); Lake Palomas, Mimbres Valley, April 14, 1892, *E. A. Mearns* (no. 184, f.; W.; also no. 183 in 1892 without exact locality, fr.; N.).—State of Sinaloa, vicinity of San Blas, March 24, 1910, *Rose*, *Standley*, and *Russell* (no. 13415, f., fr.; N., W.).

C. R. BALL, in describing *S. Gooddingii* from rather poor female specimens, mistook it for a species of sect. LONGIFOLIAE. Later he recognized, as he has told me, the identity of his species with *S. nigra* var. *vallicola* Dudl. (*S. vallicola* Britt.). According to the international code the name *S. Gooddingii* has to be used if this willow is considered a distinct species. It certainly is a good species, and very different from the eastern *S. nigra*, which always has more or less reddish brown or purplish branchlets. Otherwise, the western species is closely related to *S. nigra*, and is clearly a member of the same section.

Sect. II. TRIANDRAE Dumortier in Bijdr. Natuurk. Wetensch. **1**:58 (Verh. Gesl. Wilgen 17). 1825; Borrer in Hooker, Brit. Fl. 414. 1830; in Loud., Arb. Frut. Brit. **3**:1496. 1838, excl. *S. lucida*.—Sect. AMYGDALINAE W. D. Koch, Salic. Eur. Comment. 17. 1828, pro parte; Andersson in K. Sv. Vet.-Akad. Handl. **6**:19 (Mon. Salic.). 1867, pro parte; in DC. Prodr. **16**^{2}:200. 1868, pro parte; Ball in Coult. and Nels., New Man. Rocky Mt. Bot. 129. 1909, excl. *S. nigra*.

In my opinion, *S. amygdaloides* And. is the only American willow which belongs to this section. It seems to be more closely related to the European-Asiatic *S. amygdalina* L. than to *S. nigra* with which it is usually associated in the same section by authors.

4. S. AMYGDALOIDES, var. **Wrightii** Schn., comb. nov.—*S. Wrightii* And. in Oefvers. K. Vet.-Akad. Förh. **15**:115 (Bidr. Känned. Nordam. Pilart.). 1858; in Proc. Amer. Acad. **4**:55 (Sal. Bor.-Am. 9). 1858; in Walp., Ann. Bot. **5**:745. 1858; *S. nigra* ***S. *Wrightii* And. in K. Sv. Vet.-Handl. **6**:22. 1867; *S. nigra* b. *latifolia γ brevifolia testacea* And., l. c. 21; *S. nigra δ Wrightii* And. in DC. Prodr. **16**^{2}:201. 1868; Hemsl. in Biol. Centr. Am. Bot. **3**:180. 1883, quoad Wright 1877[8]; Bebb in Bot. Gaz. **16**:102. 1891; *S. testacea* And., in Prodr. l. c., pro synon. *S. nigrae* formae 3.

TYPE LOCALITY.—Western Texas, El Paso County, or, according to WOOTON and STANDLEY, Mexico, state of Chihuahua, on the Upper Rio Grande or from Lake Santa Maria (coll. *C. Wright* no. 1877).

RANGE.—Western Texas near the border of Mexico and probably adjacent Mexico, northern New Mexico (and ? southern Colorado).

SPECIMENS EXAMINED.—Besides C. Wright's nos. 1876 and 1877, which may have been collected in Chihuahua in the places mentioned above, I have not seen any specimen from Mexico.

Judging by the material before me, *S. Wrightii* seems to be hardly more than a variety of *S. amygdaloides*, from which it differs chiefly in its more distinctly yellowish branchlets, its more lanceolate and more gradually acuminate leaves which always possess numerous stomata in the upper epidermis. It is certainly not a "mere forma monstrosa" as BEBB suggested in Gard. and For. **8**:363. 1895; and as is stated even by BALL in Coult. and Nels., New Man. Rocky Mt. Bot. 129. 1909, who, however, regards it now as a good species. The type specimen, *Wright* no. 1877, shows short, dense, and indeed not quite normal fruiting aments, which when well developed measure up to 10 cm. in length. *Wright* no. 1876, the type of what ANDERSSON called *S. nigra latifolia brevifolia testacea*, a specimen with male and female flowers and very young leaves, has been erroneously regarded by some authors as being the same as *S. nigra longipes venulosa* And. The type of this form which I have not seen from Mexico is *Wright* no. 1879. It represents the southwestern variety of *S. longipes* Shuttl. (*S. occidentalis* Bosc apud Koch, non Walter) and has to be called *S. longipes*, var. **venulosa** (And.) Schn., n. comb.

[8] The second specimen mentioned by HEMSLEY, which had been collected by *Jurgensen* (no. 307) in the "Sierra San Pedro Nolasco" (? state of Oaxaca), does not belong to our variety, but I have not seen it.

Sect. III. BONPLANDIANAE Schn., sect. nov.—Sect. AMYGDALINAE And. in K. Sv. Vet.-Akad. Handl. **6**:19 (Mon. Salic.). 1867, pro parte; in DC. Prodr. **16**^{2}:200. 1868, pro parte.—Arbores vel frutices alti. Folia mediocra vel satis magna, pleraque anguste vel late lanceolata vel elliptico-lanceolata, adulta crasse papyracea, superne non stomatifera. Amenta coetanea vel serotina, mascula brevi-pedunculata vel rarius sessilia, cylindrica, interdum satis longa, densi- vel sublaxiflora, floribus pleiandris, staminibus 3–7(–11), antheris pl. m. globosis, glandulis 2, saepe lobulatis vel partitis et pseudodiscum formantibus rarius distinctis dorsali interdum parva; amenta feminea pleraque longius pedicellata, fructifera saepe elongata, pleraque densiflora; ovaria longe (rarius breviter) pedicellata, glabra vel (saltem partim) pilosa; styli breves vel brevissimi, stigmatibus satis brevibus clausis vel emarginatis; glandula una ventralis, saepe lata, truncata et satis crassa, interdum basim pedicelli subamplectens.[9]

The species united by me in this section form a very distinct group of the American PLEIANDRAE. They are closely related among each other, but well separated from the other sections of the PLEIANDRAE either in America or in the Old World. In some respects they somewhat resemble the species of sect. TETRASPERMAE And. sensu SCHNEIDER in Sargent, Pl. Wilson **3**:93. 1916, but I am far from assuming that there may be a close relationship between those two sections. A main difference between the species of sect. BONPLANDIANAE and most of the other American PLEIANDRAE is the complete absence of stomata in the upper surface of the

[9] With regard to these glands the following is to be said. In SARGENT, *Silva N. Am.* **9**:120. 1896, we find the statement that *S. Bonplandiana* (var. *Toumeyi*) has a "cup-shaped disk," and that it is the only willow of the United States with a cuplike disk. Besides this, SARGENT says that this disk "is not represented in ANDERSSON'S figure" (Mon. Salic. *pl. 1, fig. 14*), but in ANDERSSON'S *fig. 14, d* the disk is well shown. Referring to the figure given in SARGENT (*pl. 472*), TOEPFFER (Österr. Bot. Zeit. **54**:175. 1904) says that there is in *S. Bonplandiana* "ein vollkommen becherförmiger Torus, wie bei der Gattung *Populus*." This is, however, not the case. After having investigated the flowers of the specimens mentioned above, I find that there is only a large and broad ventral gland which sometimes almost entirely encircles the base of the pedicel, but mostly there is a distinct lack of a dorsal gland. The very same conditions may be observed in specimens of the typical *S. longipes* Shuttl. from Florida. The broad, half-embracing ventral gland is very rarely nearly cup-shaped and somewhat similar to the cuplike torus of *Populus*.

leaves. Probably all the other PLEIANDRAE possess such stomata, but sometimes they are so sparse that it is difficult to detect them.

5. S. JALISCANA Jones, Contrib. West. Bot. **12**:77. 1908.—Ad descriptionem addenda et emendanda: Frutex ut videtur altus; truncus?; ramuli novelli dense griseo- vel subferrugineo-villosulo-tomentosi, annotini fuscescentes, laxius vel tantum partim tomentosuli, vetustiores fusco-cinerascentes, glabrescentes. Gemmae bene evolutae non visae, ut videtur glabrae. Folia matura perfecte evoluta a me non visa, semievoluta (in specimine femineo) inferiora ovali-elliptica vel elliptico-obovata, superiora majora elliptica vel elliptico-lanceolata, basi obtusa rotundave, apice acuta vel summo breviter acuminata, inferiora ut videtur satis evoluta (minimis exceptis) 3.5:1.5 ad 5.5:2.3 cm. magna, superiora ad 7:2.5 vel 8:1.7–2 cm. magna, in speciminibus masculis pleraque angustiora, interdum oblanceolata, 3:0.7 ad 8:1.5 cm. magna, superne initio pl. m. sericeo-villosa, cito glabrescentia, adulta probabiliter glabra vel tantum in costa flavescente plana pl. m. pubescentia, intense viridia, subtus valde discoloria, initio dense griseo- vel ferrugineo-villosa, dein glabrescentia, glaucescentia, pruinosa, costa nervisque lateralibus utrinsecus ad 12 angulo 60–45° a costa abeuntibus versus marginem currentibus pl. m. prominulis flavescentibusque, margine pl. m. dense subdistincte glanduloso-serrato-denticulata, versus basim integerrima. Petioli 1–8 mm. longi, superne sulcati, undique villoso-tomentelli. Stipulae parvae, lineari-lanceolatae, subglabrae, denticulatae, petiolis 2–3plo breviores, cito deciduae. Amenta tardiva, ramulos normaliter foliatos 1–2 cm. longos terminantia, rhachi villosa; mascula cylindrica, ad 3.5:0.8 cm. magna, densiflora; bractae obovatae vel late ovato-oblongae, obtusae vel rotundatae, flavescentes, utrinque villosae vel apicem versus glabrescentes, 2–3.5 mm. longae; stamina pleraque 5, filamentis ad medium fere villosis, antheris flavis elliptico-globosis; glandulae 2, pl. m. lobatae, rarius simplices; amenta feminea semimatura ad 4.5 cm. longa et 1.3–1.5 cm. crassa, cylindrica vel elliptico-cylindrica, fructibus valde congestis; bracteae late oblongae, obtusae, villosulae, apice glabriores, pedicellum paullo vel vix superantes; ovaria semimatura (juvenilia ignota) ovoideo-conica, basi subacuta, apice obtusa, circ. 4 mm.

longa, basi et pedicello subcrasso iis subduplo breviore pilosa, ceterum glabra, stylo brevi stigmatibus brevibus subbifidis satis latis vix longiore coronata; glandula 1, late ovato-rectangularis, quam pedicellus 3(–4)plo brevior, satis crassa.

TYPE LOCALITY.—Mexico: State of Jalisco, Ferreria, and Sierra de Nayarit.

RANGE.—As above, possibly also in Terr. Tepic, to which part of the Sierra de Nayarit belongs (probably also in the state of Michoacan, see note below).

SPECIMENS EXAMINED.—Mexico: State of Jalisco, Sierra de Nayarit, without date, *Léon Diquet* (male paratype; N.); Ferreria, May 28, 1898 (2?), *M. E. Jones* (no. 437; female type of description, probably also co-type of Jones, who gives no number and as year 1892; M.); without any locality or date, *G. H. G[raham]*[10] (m., ex Herb. J. S. Mill in Herb. G.; identical with Diquet's specimen).

The specimens before me agree well with JONES's description, who collected only the female plant. No. 437 is very likely the same as the plant cited by him as type. It seems to me more closely related to *S. Bonplandiana* or *S. longipes* than to *S. laevigata* mentioned by JONES. Unfortunately, there are no fully grown leaves; the largest I have seen resemble those of *S. longipes*. In size and shape of the female aments and of the fruits it comes very near *S. Bonplandiana*. The male aments are remarkably small and fine, hardly as long or longer than the narrowly lanceolate leaves of the peduncle.

6. S. BONPLANDIANA Kunth in Humboldt and Bonpland, Nov. Gen. Pl. **2**:20. *pls. 101, 102.* 1817; Syn. Pl. Aequin. **1**:365. 1822; Martens and Galeotti in Bull. Acad. R. Bruxelles **10**[1]:343 (Enum. Pl. Galeot. Mex. 3). 1843; Andersson in K. Sv. Vet.-Akad. Handl. **6**:18, *pl. 1, fig. 14* (Mon. Salic.). 1867, excl. var.; in DC. Prodr. **16**[2]:200. 1868, excl. var.; Hemsley in Biol. Centr. Am. Bot. **3**:179. 1883, excl. var.; Brandegee in Proc. Cal. Acad. Sci. II. **3**:173. 1891; Wooton and Standley in Contrib. U.S. Nat. Herb. **19**:161 (Fl. N.Mex.). 1915; Goldman in Contrib. l. c. **16**:320. 1916.

TYPE LOCALITY.—"In regno Mexicano locis opacatis prope Moran, Cabrera, Omitlan et Pachuca,[11] alt. 1270–1350 hexap." (coll. *Humboldt* and *Bonpland*, ex Kunth).

[10] According to BENTHAM, Pl. Hartw. preface p. 4. 1839, GRAHAM collected "about the town of Mexico and in the mining district of Tlalpuxahua and Real del Monte." Tlalpuxahua is in the state of Michoacan, 50 miles east of Morelia.

[11] These localities are probably all in the state of Hidalgo; see Humb. and Bonpl., Nov. Gen. Pl. 7:341. 1825.

RANGE.—The typical form extends from the southwestern corner of New Mexico through the states of Chihuahua, Durango, southern Coahuila, southern Lower California, to Oaxaca and Vera Cruz, and probably farther south in Mexico, because the species occurs again in Guatemala (see below); see also under var. *Toumeyi*.

SPECIMENS EXAMINED.—New Mexico: Grant County, Canyon east side of San Luis Mountains, September 11, 1893, *E. A. Mearns* (no. 2189, m.; M., N.).—Mexico: State of Chihuahua, Canyon below Cusihuiriachic, September 21, 1888, *C. G. Pringle* (no. 2003, m., fr.); in the Sierra Madre near Seven Star Mine, alt. 2300 m., September 4, 1899, *C. H. T. Townsend* and *C. M. Barber* (no. 405, f., fr.; G., M.; forma porro observanda, an ad var. *Toumeyi* referenda?).—State of Coahuila, Jaral, [?June] 10, 1886, *W. Schumann* (no. 1318, m.; W.).—State of Durango, vicinity of Durango, [autumn] 1896, *E. Palmer* (no. 636, f., fr.).—Lower California, near Creek San Pablo, alt. 180–220 m., January–March 1898, *C. A. Purpus* (no. 140, m., fr.; W.); from El Saccaton to Cape San Lucas, alt. 10–150 m., December 29, 1905, *E. W. Nelson* and *E. A. Goldman* (no. 7373, m.; W.); from Miraflores to San Bernardo Ranch in Sierra La Laguna, alt. 450 m., January 20, 1906, same coll. (no. 7419, m.; W.).—State of San Luis Potosi, "ex convalli San Luis Potosi," 1877, *J. G. Schaffner* (no. 263, f.; N.).—State of Hidalgo, Tula, river banks, alt. 2000 m., August 18, 1906, *C. G. Pringle* (no. 13788, m., f.; G., W.).—State of Queretaro, near San Juan del Rio, August 18, 1905, *J. N. Rose*, *J. H. Painter*, and *J. G. Rose* (no. 9600, fr.; N.).—State of Guanajuato, Guanajuato, September and November 1897, *A. Dugès* (m., fr.; G., W.).—State of Jalisco, Guadaljara, February 28, 1907, *W. E. Safford* (no. 1425, st.; W.; "an important tree planted for shade"); near Tequila, July 5–6, 1899, *J. N. Rose* and *W. Hough* (no. 4768, im. fr.; W.).—State of Michoacan, valley near Zinapecuaro, east of Morelia, May 2, 1849, *J. Gregg* (no. 767, st.; M.; "tree 30 ft. high"); wet places near Patzcuaro, November 20, 1890, *C. G. Pringle* (no. 3376, m., f.).—Federal District, "Vallée de Mexico," June 18, 1865, *E. Bourgeau* (no. 423, m., f.; G., W.); same locality, alt. 2200 m., August 17, 1901, *C. G. Pringle* (no. 9337, m., f., fr.; G., M., W.); also August 12, 1899, *C. G. Pringle* (no. 7916, m., f.; G.; "small tree"); without exact locality, September 16, 1910, *C. R. Orcutt* (no. 4070, m.; M.); without any locality but probably in this district, *G. J. G*[*raham*] (m.; G.).—State of Morelos, by streams near Cuernavaca, alt. 1500 m., August 14, 1906, *C. G. Pringle* (no. 10284, m., f.; G., M., W.); also June 9, 1904, *C. G. Pringle* (no. 13203, m., f., fr.; G., W.).—State of Puebla, Tehuacan, *H. Galeotti* (no. 67, m.; N.).

The typical *S. Bonplandiana* is a well marked species which produces its flowers in the axils of the mature leaves from July to January, the old leaves not falling off until the new growth starts. This habit gives the species a peculiar appearance, but cannot be regarded as a valuable taxonomic character because it seems due to climatic conditions. The following specimens from Guatemala, therefore, hardly represent a different variety but only a

form the flowers of which appear with the development of the young leaves. Nevertheless, this most southern form of *S. Bonplandiana* needs further observation. The young twigs and the upper surfaces of the young leaves show a scanty pubescence of rather long downy silky hairs. TUERCKHEIM's specimens have been regarded as belonging to *S. laevigata* by BEBB, but in my opinion they are much more similar to *S. Bonplandiana* than to the other species.

Guatemala: Dept. Alta Verapaz, "am Cobanflusse bei Coban," alt. 1360 m., February 1886, *A. v. Tuerckheim* (no. 333, m., f.; G., W.; ab J. D. SMITH sub nomine *Humboldtiana falcata* distributa, praeterea a cl. BEBB *S. laevigata* nominata); same place, alt. 1360 m., November 1907, *A. v. Tuerckheim* (no. II. 1526, f., fr.; G., M., W.; eadem forma ac no. 333 sed folia novella superne laxe sericeo-villosa cito glabrescentia).—Dept. Baja Verapaz, between Tactic and Salancá, June 5, 1904, *O. F. Cook* (no. 217, st.; W.)—Dept. Huehuetenango, roadside near Huehuetenango, alt. 1950–2600 m., January 10–11, 1896, *E. W. Nelson* (no. 3677, m.; W.).—Dept. Solalá, San Lucas, February 15–16, 1906, *W. A. Kellerman* (nos. 5693, 5819, st.; W.); Volcano of Santa Maria, alt. 2600–3500 m., January 24, 1906, *E. W. Nelson* (no. 3725, f., fr.; G., W.).—Dept. Sacatepequez, Santa Maria de Jesus, cult. in hedge, February 18, 1905, *W. A. Kellerman* (no. 4528, st.; W.).

6b. S. BONPLANDIANA, var. PALLIDA And. in DC. Prodr. **16**[2]:200. 1868; Hemsley in Biol. Centr. Am. Bot. **3**:179. 1883; Brandegee in Proc. Cal. Acad. Sci. II. **2**:205. 1889, fide auctor; Bebb apud Vasey and Rose in Contrib. U.S. Nat. Herb. **1**:77. 1890.—*S. pallida* Kunth in Humb. and Bonpl., Nov. Gen. Pl. **2**:20. 1817; *S. Bonplandiana* **S. pallida* And. in K. Sv. Vet.-Akad. Handl. **6**:18 (Mon. Salic.). 1867.

A typo nonnisi recedit ramulis novellis petiolisque satis vel parce villosulis foliis etiam saepe ad costam pl. m. pilosis.

TYPE LOCALITY.—"In calidis regni Novae Hispaniae inter Venta de Acaguisotla et Masatlan[12]) alt. 500–650 hexap." (coll. *Humboldt* and *Bonpland*, ex Kunth).

RANGE.—Central Mexico (probably also in Lower California).

SPECIMENS EXAMINED.—State of San Luis Potosi, without exact locality, 1877, *J. G. Schaffner* (no. 263, f.; W.); "in locis cultis circa urbem San Luis Potosi," 1876, *J. G. Schaffner* (no. 895 partim, f.; G.; mixed with sterile specimen of *S. Humboldtiana* var. *stipulacea*).—State of Puebla, Atlixco, July 25, August 1, 1893, *E. W. Nelson* (m.; W.; ramulis tantum apice parce pilosis).—State of Jalisco, near Huejuquilla, August 24, 1897, *J. N. Rose* (no. 2535, m.;

[12] These localities which I cannot find on the maps at my disposal seem to be in the state of Guerrero according to Humb. and Bonpl., Nov. Gen. Pl. **7**:341. 1825.

W.; ut praecedens).—State of Oaxaca, Valle de Etla, alt. 1580 m., April 1906, *C. Conzatti* (no. 1721, fr.; W.).

It is on the authority of ANDERSSON that I refer these specimens to var. *pallida*. Without having seen a type specimen I cannot decide whether KUNTH'S species really represents a variety of *S. Bonplandiana*. The specimens before me are in my opinion nothing but a more or less pubescent form and hardly deserve the rank of a variety. The geographical distribution is probably the same as that of the species. Almost every species of the American PLEIANDRAE breaks up in a hairy and a glabrous variety which sometimes look very different, but mostly seem to be connected by every grade of intermediate forms.

6c. S. BONPLANDIANA, var. **Toumeyi** Schn., var. nov.—*S. Bonplandiana* Bebb in Gard. and For. **8**:364. 1895, non Kunth; Sargent N.Am. Silva **9**:119. *pl. 472.* 1896, exclud. syn. pro parte max.; *S. Toumeyi* Britton, N.Am. Trees 187, *fig. 145.* 1908; *S. Humboldtiana* Sarg. ex Britton, l. c., pro synon., non Willd.—Ab typo nonnisi differre videtur foliis plerisque angustioribus minus distincte denticulatis, petiolis saepissime satis brevibus vix ultra 1 cm. longis apice haud vel valde indistincte glandulosis, amentis fere semper primo vere in axillis foliorum persistentium apparentibus vel (foliis adultis delapsis) praecocibus vel coetaneis masculis brevioribus vix ultra 3 cm. longis et fructiferis vix ultra 2.5:1–2.2 cm. magnis, glandula dorsali florum femineorum interdum minima.

TYPE LOCALITY.—Southern Arizona: Pima County, Santa Catalina Mountains, Sabino Canyon.

RANGE.—Southeastern Arizona, northern Sonora and Chihuahua (? southwestern New Mexico and Lower California).

SPECIMENS EXAMINED.—Arizona: Pima County, Santa Catalina Mountains, Sabino Canyon, February 20, July 23, 1894, *J. W. Toumey* (f., fr., paratype; N.); also April 8, October 7, 1894, *J. W. Toumey* (st.); also February 15, March 12, April 8, 1894, *J. W. Toumey* (m., f., fr.; "tree 25–50 ft., deeply furrowed bark"); same place, April 10, 1901, *C. L. Shear* (no. 4201, m., fr.; type; N.); same place, alt. 800 m., August 24, 1903, *Thornber* (no. 169a, f.; M.; a forma typica *S. Bonplandianae* vix distinguenda); same place, March 30, 1901, *D. Griffith* (no. 2577, m.; N.).—Mexico: State of Sonora, Guadalupe Canyon, August 28, 1893, *E. C. Merton* (no. 2071, st.; W.; forma aliquid incerta).—State of Chihuahua, Cajou Bonita Creek, July 24, 1892, *E. A. Mearns* (no. 553, st.; W.; "a tree 80 cm. in circumference and 10 m. high"; forma porro observanda).—Lower California, without exact locality, March–June 1897, *A. W. Anthony* (fr., W.; forma aliquid incerta).

I am not sure whether this variety can be regarded as more than a mere form of *S. Bonplandiana*, but judging by the rather insufficient material before me I think it best to keep it as a variety, to which probably the specimen from southwestern New Mexico, enumerated under the type, should be referred. There is a specimen collected by *E. Palmer* in the state of Durango, at Tepehuanes, March 25–April 16, 1906 (no. 9, m.; M., W.) which looks like a pubescent form of var. *Toumeyi* corresponding with the var. *pallida* of the type.

7. S. LAEVIGATA Bebb in Amer. Nat. **8**:202. 1874; in Watson, Bot. Calif. **2**:83. 1879; Ball in Trans. Acad. Sci. St. Louis **9**:69. 1899.

I mention this willow only because its occurrence might be expected in northern Lower California, but I have not yet met with a specimen of it from this region. As I have explained, the Guatemalan willow referred by BEBB to *S. laevigata* belongs to *S. Bonplandiana*. *S. laevigata* is the western counterpart of the eastern *S. longipes*.

8. S. LONGIPES Shuttleworth apud And. in Öfv. K. Vet.-Akad. Förh. **15**:114 (Bidr. Känned. Am. Pilarter). 1858; in Proc. Amer. Acad. **4**:53 (Sal. Bor. Am. 7). 1858; in Walp., Ann. Bot. **5**:744. 1858.—*S. occidentalis* Bosc apud Koch, De Sal. Eur. Com. 16. 1828, non Walter 1788; And. in K. Sv. Vet.-Akad. Handl. **6**:23, *pl. 2, fig. 16* (Mon. Salic.). 1867; in DC. Prodr. **16**^{2}:202. 1868; Bebb in Gard. and For. **8**:364. 1895, in adnot.; Sargent, Silva N.Am. **9**:109, *pl. 465*. 1896, excl. var. pro parte; *S. subvillosa* Elliott ex Nuttall, N.Am. Silva **1**:79. 1843, nom. nud.; *S. longipes*, var. *pubescens* And. in Öfv., l. c. 114; in Proc., l. c. 53; in Walp., l. c. 744; *S. gongylocarpa* Shuttlew. apud And., l. c., pro synon.; *S. floridana* Chapman, Fl. S. U.S. 430. 1860; *S. Humboldtiana* Grisebach, Cat. Pl. Cub. 41. 1866, non Willd.; *S. nigra* ****S. longipes* And. in K. Sv., l. c. 22; excl. var. *venulosa; S. nigra* γ *longipes* And. in DC., l. c. 201. excl. *f. venulosa; S. Bonplandiana* Sauvalle, Fl. Cuba 134. 1873, non Kunth; De la Maza and Roig, Fl. Cuba 64. 1914; *S. occidentalis*, var. *longipes* Bebb in Gard. and For. **8**:363. 1895; *S. amphibia* Small, Fl. Miami 61. 1913.

TYPE LOCALITY (of *S. occidentalis* Bosc).—"In insula Cuba" (coll. *Sieber*, ex Koch).

RANGE.—The typical form, to which the synonymy given above applies, is found from Cuba to northern Florida (Duval and Wakulla counties).

SPECIMENS EXAMINED (from Cuba).—Prov. Pinar del Rio, Galafre, March 7, 1911, *N. L. Britton* and *J. F. Cowell* (no. 9839, m., st.; N., W.);

Pinar del Rio, 1911, *J. F. Cowell* (st.).—Prov. La Habana, San Antonio de los Baños, December 18, 1905, *Van Hermann* (no. 3332, fr.); Playa de Mariano, February 22, 1910, *N. L. Britton* and *P. Wilson* (no. 4521, f.; G., N., W.); Batabano, wet coastal Savanna, April 12, 1912, *N. L. Britton*, *J. F. Cowell*, and *C. de la Torre* (no. 13359, st.; N., W.).—Prov. Santa Clara, Cienaga de Zapata, March 26 [1860–64], *C. Wright* (no. 2132, m., st.; G., M., W.).—Prov. Camaguey "ad las Piedras," February 1824, *Poeppig* (f.; M.).

This species, which is well represented in the southeastern and central United States by var. **Wardii** (Bebb) Schn., nov. comb., and by var. *venulosa* (And.) Schn., is said by ANDERSSON to occur also in Trinida[d]. Beyond the borders of the United States I have only seen the specimens cited from Cuba. It seems to be entirely absent from Mexico, and I shall deal with this difficult and variable species in my final book.

Sect. IV. LONGIFOLIAE And. in Öfv. K. Vet. Ak.-Förh. **15**:116. 1858; in Proc. Amer. Acad. **4**:55 (Salic. Bor. Am. 10). 1858; in Walp., Ann. Bot. **5**:745. 1858; in K. Sv. Vet.-Akad. Handl. **6**:54 (Mon. Salic.). 1867; in DC. Prodr. **16**^{2}:214. 1868; Bebb in BOT. GAZ. **16**:103. 1891; Rowlee in Bull. Torr. Bot. Club **27**:247. 1900; Schneider, Ill. Handb. Laubh. **1**:32. 1904; Ball in Coult. and Nels., New Man. Rocky Mt. Bot. 130. 1909.

This is a well marked and entirely American section. There are no other willows closely related to those of this section, either in America or in the Old World. Probably the species of the sect. ALBAE Borr. (not of sect. FRAGILES Koch) may represent the nearest relatives to the LONGIFOLIAE. In Mexico there is only one species widely distributed; the other forms of this group mentioned later reach our territory only in its most northern parts. It may be mentioned that, according to GÄRTNER (Vergl. Blattanatomie Gatt. *Salix*, Diss. Göttingen, 1907, p. 54) *S. macrolepis* Turcz. from Northeastern Asia shows "eine so ausgesprochene Aehnlichkeit im Blattbau, dass es keinen Augenblick zweifelhaft sein kann, dass die nächsten Verwandten von *S. macrolepis* Arten wie *S. Hindsiana* und *S. longifolia* sind." I have dealt with this interesting Asiatic species in Sargent, Pl. Wilson. **3**:102. 1916, but I have seen only a poor specimen. Even if GÄRTNER has examined material of the true *macrolepis*, I am not convinced that similar anatomical characters can be taken for a proof of close taxonomic relationship in a case where the morphological characters of the flowers are, apparently, so different.

9. S. TAXIFOLIA Kunth in Humb. and Bonpl., Nov. Gen. Pl. **2**:18. 1817; Syn. Pl. Aequinoct. **1**:364. 1822; And. in Öfv., l. c. 117, excl. var. *microphylla;* in Proc., l. c. 56(11); in Walp., l. c. 746; in K. Sv., l. c. 57, pro parte; in DC., l. c. 215, pro parte; Hemsl. in Biol. Centr. Am. Bot. **3**:180. 1883; Brandegee in Zoe **4**:406. 1894; Rowlee in Bull., l. c. 249, *pl. 9, fig. 2;* Jones, Willow Fam. Gr. Plat. 25. 1908; Goldman in Contrib. U.S. Nat. Herb. **16**:321. 1916. ?*S. taxifolia*, b *lejocarpa* And. in K. Sv., l. c. 57; in DC., l. c. 215; ?*S. taxifolia a sericocarpa* And., l. c. 57; ?*S. taxifolia a sericocoma* And. in DC., l. c. 215.

TYPE LOCALITY.—"Colitur in Hortis Mexici, Queretari, Zelayae, alt. 900–1200 hex."

RANGE.—From Mexico I have seen wild specimens only from the state of Durango and Chihuahua, and also from Lower California. It is also found in southeastern Arizona, southern New Mexico, and southwestern Texas.

SPECIMENS EXAMINED.—Mexico: State of Durango, vicinity of the city of Durango, August 1896, *E. Palmer* (no. 473, m.; the specimen in the Gray Herbarium consists of two forms, the leaves of the left one being rather short and broad).—State of Chihuahua, valley near Chihuahua, October 5, 1885, *C. G. Pringle* (no. $23\frac{1}{2}$, m., f., fr.); same place, April 6, 1886, *C. G. Pringle* (no. 864, m.; W.); near Balleza, September 23, 1898, *E. H. Goldman* (m.; G.); Cajou Creek, near the U.S. Boundary line, July 2, 1892, *E. A. Mearns* (no. 398, st.; N., W.); San Pedro River, October 12, 1892, *E. A. Mearns* (no. 1111, m.; N.).—Lower California, Santa Anita (Cape Region), March 1901, *C. A. Purpus* (no. 232, m.; W.; forma satis latifolia); from San Bernardo to El Sauz, Sierra La Laguna, January 21, 1906, *E. W. Nelson* and *E. A. Goldman* (no. 7434, m.; W.); Corral Piedra, September 9, 1893, *J. G. Brandegee* (f.; W.).—Without exact locality, 1846, *T. Hartweg* (no. 391, m.; ex Herb. Hooker in Herb. N.).

I have not yet seen a type specimen of the typical *S. taxifolia* of which HUMBOLDT and BONPLAND apparently collected only specimens of cultivated plants. All the specimens before me from central and southern Mexico belong to var. *microphylla*. The typical form seems to be restricted to the central and western part of northern Mexico, where it occurs probably, also in Sonora, and to the parts of the southern central United States mentioned.

There are the following specimens from Chihuahua which come very near typical *S. taxifolia*, but in some respects resemble *S. exigua* (var. *stenophylla*). They may be regarded as belonging to a separate form of *S. taxifolia* also represented in the United States which I am not yet able to interpret correctly. I hope I can deal with it finally in my future book. Bachimba Canyon, March 23, 1885, *C. G. Pringle* (no. 95; f.; G.); vicinity of Chihuahua, alt. about 1300 m., April 8–27, 1908, *E. Palmer* (no. 39, m.; G., M., W.). Another

specimen collected by *Wilkinson*, April 4, 1885 (m.; W.), the exact locality of which I cannot discover, shows rather large elliptic anthers.

The varieties distinguished by ANDERSSON as var. *lejocarpa* and var. *sericocarpa* (*sericocoma*) with glabrescent or densely hairy capsules I cannot identify because he does not cite any specimens. The young ovaries are always pubescent, and even the ripe fruits seem to be never wholly glabrous. See also my remarks under the following variety.

9b. S. TAXIFOLIA, var. **microphylla** Schn., nov. var.—*S. microphylla* Schl. and Cham. in Linnaea **6**:354. 1831; Hooker and Arn., Bot. Beech. Voy. 310. *pl. 70.* 1840; Mart. and Gal. in Bull. Acad. R. Brux. **10**[1]:345 (Enum. Pl. Gal. Mex. 5). 1843; Rowlee in Bull. Torr. Bot. Club **27**:249. 1900, pro parte; *S. taxifolia* And., l. c. and Hemsl., l. c. (sub *taxifolia*) pro parte, non Kunth; Loes. in Bull. Herb. Boiss. **7**:545 (Pl. Seler. 67). 1899.—A typo praecipue recedit: pubescentia ramulorum novellorum magis villosa vel fere subhirsuta, foliis ut videtur minus crassis subtus magis discoloribus distinctius sericeis interdum oblanceolatis et pro longitudine satis latis distinctius denticulatis, stipulis ovato-lanceolatis vel lanceolatis petiolo brevissimo sublongioribus, floribus masculis fere semper glandula tantum ventrali praeditis, amentis fructiferis subcrassioribus 2:1.2 cm. magnis.

TYPE LOCALITY.—Mexico, state of Vera Cruz, "ad ripam arenosam fluminis Tecolutensis prope San Pablo."

RANGE.—Central Mexico to Guatemala and Porto Rico. I have seen specimens from the states of Vera Cruz, San Luis Potosi, Coahuila, Terr. Tepic, Jalisco, Michoacan, Morelos, Puebla, Oaxaca, and from Guatemala and Porto Rico.

SPECIMENS EXAMINED.—The numerous Mexican specimens I have seen will be enumerated in my final book. Guatemala: on the river Pinula, on the road from Guatemala to Amatillan, 1845, *Skinner* (f., ex Herb. Bentham in Herb. N.).—Porto Rico: "Lago San José, près San Juan, October 1909," *Hiorámi* (m.; G.; an indigena?).

This variety is undoubtedly very closely related to the typical *taxifolia* and can hardly be regarded as a good species. The principal characters have already been stated. In *S. taxifolia* the leaves are somewhat longer, narrower, and more entire, the stipules are wanting or scarcely developed, the male flowers always possess a dorsal gland, and the fruiting aments are, usually, more slender.

The form regarded by ROWLEE as *S. microphylla* does not in my opinion fully agree with the typical one collected by *Schiede* and *Deppe* of which I have

seen a sterile co-type (Herb. M.). ROWLEE's form is apparently identical with that described and figured by HOOKER and ARNOTT, but the flowers of the only specimen seen by ROWLEE from Colima (leg. *E. Palmer*, no. 1193, January 9 to February 6, 1891; m.; G., W.) possess mostly two glands. It seems to me somewhat intermediate between the typical *taxifolia* and var. *microphylla* s. str. and needs further investigation.

10. S. EXIGUA Nutt., var.—*S. exigua* Goldman in Contrib. U.S. Nat. Herb. **16**:320 (Pl. Low. Cal.). 1916.

S. exigua Nutt. sensu latissimo is a wide spread willow from the Northwest Territories through the western United States (except along the Pacific Coast and the most of California) to Arizona, southern California, and New Mexico. In my opinion this species may be divided into several varieties which of course seem to be connected by intermediate forms. Having not yet finished my study of those forms I am not able to determine the following few specimens from Mexico with certainty. I can only enumerate them and add a few notes.

There is, first, a specimen from Lower California: Arroyo de Leon, northwest slope of the San Pedro Martir Mountains, alt. 950 m., July 4, 1905, *A. E. Goldman* (no. 1200, m.; W.). It can probably be referred to *S. exigua*, var. **stenophylla** (Rydbg.) Schn., nov. var.,[13] but owing to the absence of female flowers I am not sure of its relationship. To the same form seems to belong a male specimen from Chihuahua: along the Rio Grande, near Ciudad Juarez, 1911, *E. Stearns* (mixed in Herb. N. with a fruiting branch of *S. Gooddingii*). *C. G. Pringle's* no. 23 from the same state, Bachimba Canyon, May 30, 1885 (m.; G.), which has been distributed as *S. taxifolia*, probably represents the same form of *exigua* with early flowers which always look rather different from those appearing later in the season on longer, more leafy peduncles. The aments are very short, but the material is too insufficient to say more. At

[13] *S. stenophylla* Rydberg in Bull. Torr. Bot. Club **28**:272. 1901 has been described from Colorado as "nearest related to *S. exigua* Nutt." It is, in my opinion, not a good species, but probably more than "an inconstant form" (Ball in Coult. and Nels., New Man. Rocky Mt. Bot. 131. 1909), and I am inclined to use this name for what I call the southeastern and southern variety of *exigua*, the typical form of which seems to be confined to Nevada (and some of the adjacent counties of California), eastern Oregon, Idaho, western Montana, eastern Washington and northward; while var. *stenophylla* extends from Wyoming to eastern Nebraska (in probably a little different form), Colorado, New Mexico, Arizona, and probably northern Chihuahua. The forms from southern California and northern Lower California may be more closely related to typical *exigua*. The var. *stenophylla* differs chiefly in having folia saepe distinctius denticulata (interdum fere ut in *S. longifolia*), ovaria (vel saltem fructus) longius pedicellata pedicello glandulam saepissime 2plo superante, glabriuscula vel ab initio glabra. The oldest name for this form may be *S. Hindsiana*, var. *tenuifolia* And., Mon. p. 56, of which I have not yet seen the type (*Burke*, Snake River).

first sight *C. G. Pringle's* no. 220 from Ciudad Juarez (the former Paso del Norte), May 4, 1885 (m., f.; N.), looks very similar to *S. exigua*, var. *stenophylla*, but the stigmas are rather long and slender. This form needs special observation.

Somewhat more different are specimens from Lower California: near the Tia Juana, April 6, 1882, *M. E. Jones* (no. 3730, m., f.; N., W.), the female flowers of which have rather long stigmas more or less intermediate between those of the flowers of *S. exigua* and *S. sessilifolia* Nutt. The ovaries are glabrous and have a pedicel of about the same length as the gland. There are a few old leaves (apparently of the previous season) which closely resemble those of *S. sessilifolia*, var. **leucodendroides** (Rowlee) Schn., nov. comb. (*S. macrostachya*, var. *leucodendroides* Rowlee in Bull. Torr. Bot. Club **27**:250. *pl. 9. fig. 6.* 1900), the most southern form of *sessilifolia* Nutt. sensu lato. There may be hybrids between this variety and *exigua* in southern California and in the adjacent parts of Lower California where var. *leucodendroides* is likely also to occur. JONES'S specimens represent the early flowering form with rather shortly peduncled aments. "The peculiar swelling just below the stigma," which, according to RYDBERG, is a main feature of his *S. stenophylla*, may be observed in almost every form of *exigua*, *longifolia*, or other species of this section. The form collected by *Jones* may be identical with that of *LeRoy Abrams* on the Tia Juana River in San Diego County, California, May 14, 1903 (no. 3485, f., fr.; G.), which I can hardly distinguish from typical *exigua*.

There remains another doubtful form from Chihuahua, Puerta de St. Diego, alt. 1800 m., April 13, 1891, *C. V. Hartman* (no. 625, m.; "8–12 ft. high"), which has been distributed as *S. taxifolia*. It is a very early flowering form with small subsessile ovoid aments (6–12 mm. long) and very narrow short young leaves (up to 12 by 0.5 mm.). According to the globular anthers it may be an unusually early flowering *taxifolia;* on the other hand one might regard it as an abnormal state of *exigua stenophylla*.

11. S. LONGIFOLIA, var. ANGUSTISSIMA And. in Öfv. K. Vet.-Ak. Förh. **15**:116. 1858, excl. specim. Wrightii no. 1875; in Proc. Amer. Akad. **4**:56 (Sal. Bor. Am. 10). 1858; in Walp., Ann. Bot. **5**:746. 1858.—*S. longifolia* *** *opaca* And. in K. Sv. Vet.-Akad. Handl. **6**:55 (Mon. Salic.). 1867, quoad specim. Berlandierii no. 2341; *S. longifolia* γ *argyrophylla* And. in D.C Prodr. **16**^{2}:214. 1868, quoad specim. Berlandierii no. 2341 (sphalm. 2371); Coulter in Contrib. U.S. Nat. Herb. **2**:419 (Man. Phan. W. Texas). 1894, prob. pro parte maxima; *S. Thurberi* Rowlee in Bull. Torr. Bot. Club **27**:252. 1900; Blankinship in Rep. Mo. Bot. Gard. **18**:194. 1907.

TYPE LOCALITY.—Probably Texas, exact locality unknown to me (coll. *Berlandier*).

RANGE.—Central Texas to New Mexico (Dona Ana County) and northeastern Mexico (Coahuila and Nuevo Leon).

SPECIMENS EXAMINED (from Mexico).—State of Coahuila: Jimulco, by streams, alt. 1300 m., October 10, 1905, *C. G. Pringle* (no. 10086, m.; N., W.; "a medium sized tree").—State of Nuevo Leon: Monterey, along the stream through city, May 1891, *C. K. Dodge* (no. 132, m.; M., W.; looks somewhat like var. *angustissima*×*S. taxifolia*).

This willow seems to me very closely related to *longifolia* and apparently connected with it by intermediate forms. I do not regard it as a distinct species, but I cannot agree with WOOTON and STANDLEY, in Contrib. U.S. Nat. Herb. 19:160 (Fl. N.Mex.). 1915, that "*S. Thurberi* Rowlee is a form [of *exigua*] with longer leaves that are noticeably dentate," and that "it is not essentially different from *S. exigua*" as understood by these authors. The main difference of var. *angustissima* from typical *longifolia* is the absence of a dorsal gland in the male flowers and the dense silvery silky (shining) pubescence of the young ovaries. The leaves of the fertile branchlets are up to 4–8 cm. long and 1.5–5 mm. wide. The dentation and nervation are those of typical *longifolia*.

ROWLEE made a mistake in attributing all his specimens of *Thurber* (nos. 2368, 95, and 2341 in the Gray Herb.) to *G. Thurber*. Only no. 95 was collected by *Thurber*, while nos. 2341, 2368 are numbers of *Berlandier* and have been cited by ANDERSSON with nos. 911 and 3019 as the co-types of his var. *angustissima*, a fact not mentioned at all by ROWLEE.

There is a sterile specimen from the state of Durango, alluvial valley of Rio Nazas, April 14, 1847, *J. Gregg* (no. 442; M.), which may belong to our variety. The young leaves measure up to 7 cm. in length and 6 mm. in width.

There remains another specimen of a willow of this section from Lower California, ?Causito, May 20, 1883, *C. R. Orcutt* (no. 1180, fr.; M.; distributed as *longifolia*), which possibly represents the form called *S. Parishiana* by ROWLEE in Bull. l. c. 249. Unfortunately I have not yet had the opportunity to examine the types of ROWLEE'S species, collected by *F. W. Hobby* in southern California, San Bernardino County, Matilija Canyon (nos. 54, 55). As far as I can judge by the somewhat inexact description and by the material I have seen from southern California, *S. Parishiana* might be regarded as a species intermediate between *exigua* and *sessilifolia leucodendroides*, differing from the latter in the narrower, more glabrescent leaves and the shorter and slenderer fruiting aments, and from the former in the longer, narrower, more linear lobes of the stigma mostly borne by a short style. *Orcutt's* specimen has short old fruiting aments measuring not over 2 cm. in length and 8 mm. in thickness. According to ROWLEE'S statement in his description, the aments are "2–3 cm. long by 1–2 cm.," but in the key he says "aments medium size, 3 cm. or more in length."

Sect. V. SALICES DIANDRAE, excl. LONGIFOLIAE.[14]

12. S. HARTWEGII Bentham, Pl. Hartw. 52. 1840; Hemsl. in Biol. Centr. Am. Bot. **3**:180. 1883.—*S. humilis* **S. Hartwegii* And. in K. Sv. Vet.-Akad. Handl. **6**:112, *pl. 6, fig. 62** (Mon. Salic.). 1867; *S. humilis* δ *?Hartwegii* And. in DC. Prodr. **16**²:236. 1868.—Ad descriptionem brevem auctoris addenda et emendanda: habitus?, ramuli hornotini (autumno floriferi) pl. m. dense griseo- vel flaves-centi-tomentelli, angulati, versus basim et annotini purpureo-fusci glabriusculi, vetustiores ut videtur glabri, lenticellis late ellipticis flavis paucis conspersi. Gemmae foliiferae ovatae sed rostratae, ventre subapplanatae, lateraliter leviter carinatae, glabrae vel apice sparse pilosae, ad 8 mm. longae. Folia elongato-lanceolata vel anguste elliptico-lanceolata, basi acuta vel subobtusa, satis subito in petiolum contracta, apice acuta vel brevissime tenuiter acuminata, 3.5:0.7 ad 9.5:1.6 cm. magna, superne intense viridia, ut videtur nitidula, initio etiam in facie sparse (an densius?) pilosa, dein tantum ad costam subprominentem (et partim ad nervos laterales) tomentella, subtus discoloria, glaucescentia vel cinerascentia, pruinosa, initio pl. m. dense dein tantum ad nervos prominulos axillasque subbrunnescenti- vel griseo-villosulo-tomentella, costa elevata glabrescente, margine breviter et versus apicem distinctius glanduloso-denticulata. Petioli 2–8 mm. longi, superne sulcati, basi dilatati, undique tomentelli. Stipulae in ramis novellis satis distinctae, semicordatae, acutae, ad 7 mm. longae, glanduloso-denticulatae, ut folia pilosae. Amenta autumno in axillis foliorum adultorum apparentia, sessilia, brevia, densiflora, rhachi villosa, basi perula gemmarum suffulta; mascula ad 1.8:0.7 cm. magna; bracteae oblongae, apice truncatae, brunnescentes, praesertim ad basim utrinque longe pilosae; stamina 2, filamentis glabris liberis dein bracteas duplo superantibus; glandulae duae, ventralis ovato-rectangularis, quam bractea 3–3½plo brevior, dorsalis minor; amenta feminea ad 2:1 cm. magna, ut videtur recurvata; ovaria ovato-lanceolata, in stylum distinctum iis circ. 4–5plo breviorem

[14] I do not refer the following species to distinct sections because I do not yet know how to limit those sections to which these Mexican species belong. Some of them are very little known, and it needs further investigation to decide the question whether or not the species nos. 11–13 may form a special section on account of the dorsal gland present in the male flowers.

attenuata, pedicellis dimidio ovarii sublongioribus suffulta, glabra, stigmatibus linearibus bifidis stylo subaequilongis coronata; glandula 1, ovato-rectangularis, obtusa, pedicello 2–3plo brevior; bracteae oblongae, obtusae, ut in floribus masculis pilosae, pedicellum subsuperantes; fructus e basi subacuta ovoideo-lanceolati, subrostrati, circ. 4 mm. longi, pedicello 1.5–2 mm. longo excluso.

TYPE LOCALITY.—Mexico: State of Michoacan, prope Aganguio.

RANGE.—Central Mexico: States of Michoacan and Mexico.

SPECIMENS EXAMINED.—Mexico: State of Michoacan, "prope Aganguio," 1840, *Th. Hartweg* (no. 390, m.; co-type in Herb. N.).—State of Mexico, north slope of Volc. Toluca, September 9, 1893, *E. W. Nelson* (no. 26, f., fr.; W.).

This species seems most closely related to *S. mexicana* Seem., both possessing a dorsal gland in the male flowers. The late time of flowering cannot be regarded as a valuable taxonomic character because there are spring flowering forms of *S. mexicana*, and of *S. lasiolepis* I have seen forms of southern California flowering in the fall. The relationship of *S. Hartwegii* and the following species to *S. lasiolepis* and other species of sect. CORDATAE needs further investigation.

13. S. MEXICANA v. Seemen in Bot. Jahrb. **21**, Beibl. 52:9. 1895.

TYPE LOCALITY.—Mexico: State of Hidalgo, Zacualtipan[15] (coll. *Berlandier*, ex Seemen).

RANGE.—Central Mexico: States of Hidalgo, Mexico, Pueblo.

SPECIMENS EXAMINED.—Mexico: State of Hidalgo, Sierra de Pachuca, by brooks, alt. 2900 m., September 8, 1899, *C. G. Pringle* (no. 8237, f., m., st.; "10 to 15 ft."); same locality, alt. 2800 m., September 1, 1906, *C. G. Pringle* (no. 13783, m., f.; G., W.); Tulancingo, August 26, 1893, *E. W. Nelson* (m.; W.).—State of Puebla, Barranca below Honey Station, alt. 1680 m., September 9, 1906, *C. G. Pringle* (no. 13817, st.; G.).—State of Mexico, Ixtaccihuatl, along brooks, March 1906, *C. A. Purpus* (no. 1801, f., st.; G., M., W.).

The specimens before me agree well with v. SEEMEN'S description, and the Sierra de Pachuca is not far from the type locality. SEEMEN himself states that his species is closely related to *S. Hartwegii* (see above); especially by the presence of a dorsal gland which, however, is not mentioned by SEEMEN. It may easily be distinguished from *S. Hartwegii* by its glabrous branchlets and leaves, but the ovaries are glabrous in both the species, not hairy in *S. Hartwegii*, as SEEMEN states. The male specimen of *Nelson* shows a few remaining

[15] SEEMEN cites also "St. Pietro et St. Paulo (*Ehrenberg, Uhde*)." There are many localities of this name in Mexico, and not having seen the specimens I am not sure about the exact place where they were found.

hairs near the buds on the branchlets, a more distinct grayish silky pubescence of the bracts, and a very small dorsal gland.

14. **S. Schaffnerii** Schn., spec. nov.—Habitus (?), ramuli hornotini dense griseo-villoso-tomentelli, pl. m. angulati, obscure flavescentes, annotini fuscescentes, paullo glabrescentes, vetustiores purpureo-fusci, ut videtur haud omnino glabrescentes. Gemmae foliiferae ovato-oblongae, adpressae, ventre applanatae, acutae, pl. m. villoso-tomentellae, subfuscae, ad 6 mm. longae, floriferae crassiores obtusioresque. Folio adulta subcoriacea, satis crassa, inferiora minora elliptico-oblonga, superiora longiora elliptico-lanceolata, basi acuta vel obtusiora, satis subito in petiolum contracta, apice breviter acuta, inferiora obtusiora 3:1.4 ad 6:1.5–1.8 cm., superiora 6:1 ad 8:1.8 vel 9.5:1.3 cm. magna, superne ut videtur obscure viridia, novella satis villoso-tomentella, dein costa vix prominula nervisque lateralibus planis exceptis subglabrescentia, subtus pruinosa, tomento densi griseo-flavescenti obtecta, costa nervisque lateralibus prominentibus in foliis adultis interdum partim glabrescentibus flavescentibus, rete nervillarum satis distincte subprominente, margine pl. m. distincte et satis irregulariter subcrenato-denticulata. Petioli 5–10 mm. longi, superne basi dilatata excepta convexi vel plani, omnino tomentelli. Stipulae minimae, deciduae, semi-ovato-lanceolatae, acutae, dense pilosae. Amenta tantum feminea visa, (ut videtur in autumno) in axillis foliorum adultorum apparentia, sessilia, basi perula gemmarum dein decidua suffulta, elliptico-oblonga, florifera ad 1.5 cm. longa et 0.8 cm. crassa (frucifera majora?), densiflora, rhachi villosa; ovaria ovato-lanceolata, glabra vel sparse pilosa, in stylum distinctum apice breviter bifidum medio ovarii aequilongum producta, pedicello distincto ovario subaequilongo glabro vel sparse piloso suffulta, stigmatibus minimis stylo sub 4plo brevioribus breviter emarginatis; bracteae obovato-oblongae, discolores, apice rotundatae, utrinque (saltem extus) pilis longis bracteam $\frac{1}{2}$plo superantibus praeditae; glandula 1, satis parva, ovato-oblonga, apice satis obtusa, pedicello 5–6plo brevior.

TYPE LOCALITY.—Mexico: "in convalli San Luis Potosi."

RANGE.—Central Mexico: State of San Luis Potosi, probably also in Vera Cruz.

SPECIMENS EXAMINED.—Mexico: State of San Luis Potosi, "ex convalli S.L.P.," 1877, *J. G. Schaffner* (no. 265, f., type; N.).—State of Vera Cruz, "in montibus San Miguelito,"[16] 1876, *J. G. Schaffner* (no. 894, f.; G.).

From *S. Hartwegii* this species is easily distinguished by the characters given in the key. Unfortunately, I have seen only female specimens, according to which it seems to be most closely related to *S. lasiolepis*, of which I have seen a form of southern California with half-evergreen leaves, the aments appearing in the axils of the remaining leaves. But this species differs in the almost glabrous or much less pubescent leaves, in the longer cylindrical flowering aments, and in the longer gland which is two-fifths to one-half as long as the pedicel.

15. S. LASIOLEPIS Benth., Pl. Hartweg. 335. 1857.

TYPE LOCALITY.—California: "ad ripas fluviorum Salinas et Carmel prope Monterey" (coll. *Hartweg*, no. 1955).

RANGE (in Mexico).—States of Coahuila, Chihuahua, Lower California.

SPECIMENS EXAMINED.—Lower California: Nachoguero Valley, June 4, 1894, *L. Schoenfeldt* (no. 3426, fr.; W.); La Laguna, Sierra La Laguna, alt. 1650 m., January 27, 1906, *E. W. Nelson* and *E. A. Goldman* (no. 7462, m.; W.).—State of Chihuahua: Valley near Chihuahua, March 3, October 4, 1866, *C. G. Pringle* (no. 709, m., fr., st.; distributed as *S. irrorata* And.).—State of Coahuila, mountains near Saltillo, San Lorenzo Canyon, by brooks, alt. 2100 m., April 12, 1906, *C. G. Pringle* (no. 10210, fr., st.; G., M., W.; distributed as *S. Hartwegii* Benth.).

I refer these specimens to *S. lasiolepis* mostly on the authority of C. R. BALL, who determined the sheets of the Washington Herbarium. He has already made an extensive study of the species and forms of the sect. CORDATAE.

16. **S. Rowleei** Schn., nov. spec.—*S. cana* Rowlee in BOT. GAZ. **27**:137. 1899, ut videtur pro parte, non Mart. and Gal.—Planta feminea (no. 13204 Pringlei, no. 680 Greggii): Frutex altus vel arbor ad 6 m. alta; ramuli novelli dense incano-villosuli, annotini floriferi nigro-fusci, paullo glabriores (tomento cano partim obtecti), subangulati, vetustiores pl. m. glabrescentes. Gemmae ut videtur ovato-oblongae, obtusae, tomentellae, bene evolutae

[16] There are two places of this name in Mexico according to Rand McNally's map, one in Jalisco, the other and apparently more prominent in Vera Cruz, about 55 km. west of the peak of Orizaba. HEMSLEY in Biol. Centr. Am. Bot. IV:134. 1887. states that "Wilhelm" Schaffner has sent plants to Dr. Gray "from the neighbourhood of San Luis Potosi" and that he collected also at Orizaba but not in Jalisco. This "Wilhelm" Schaffner is undoubtedly the same as "Dr. J. G. Schaffner" as printed on the labels before me.

ignotae. Folio (matura ignota) elliptica, vel minora ovalia et maxima elliptico-lanceolata, apice acuta, basi acuta vel obtuse cuneata, majora 4:2 ad 7.5:3 cm. magna, superne tantum valde initio subfloccoso-villosa, cito costa nervisque lateralibus (in parte versus costam) subtomentellis exceptis glabrescentia, viridia, subtus initio distinctius subflavescenti-villosa, cito glabrescentia, valde discoloria, albo-coerulea, pruinosa, costa flava pl. m. nervis nervillisque prominulis fere omnino glabris, margine integerrima vel distanter indistincte glanduloso-denticulata. Petioli cano-villosuli, 2–8 mm. longi. Stipulae visae minimae, semiovatae, denticulatae, vix 2 mm. longae. Amenta juvenilia (no. 680 Greggii) circ. ad 3:1 cm. magna, coetanea, pedunculo foliola 3–5 parva ceterum normalia gerente ad 1 cm. longo suffulta, fructifera (no. 13204 Pringlei) 5–8(–9) cm. longa (pedunculo excluso) et ad 1.5 cm. crassa, rhachi villosa. Ovaria ovoideo-conica, pedicello iis duplo breviore incluso glabra, stylo brevi sed distincto apice paullo bifido stigmatibus oblongis bifidis sublongiore coronata; bracteae oblongae, obtusiusculae, pedicellum circ. $\frac{1}{4}$ superantes, brunnescentes, utrinque satis laxe sericeo-lanatae; glandula 1, pedicello triplo brevior, rectangularis, apice truncata vel subbifida; fructus rostrati, pedicello 4plo breviore incluso ad 8 mm. longi, valvis apertis recurvatis.—Planta mascula (no. 8047 Pringlei): ramuli et folia juvenilia (semievoluta) ab iis plantae femineae vix diversa sed folia distinctius glaucescentia. Gemmae in ramulo sterili in herbario Grayi addito ovato-oblongae, ventre applanatae, apice subrostratae, dense subflavescenti-villosulo-tomentellae, subadpressae, ad 12 mm. longae. Amenta pl. m. praecocia, subsessilia, ad 4.5:1.5 cm. magna, pedunculo ad 8 mm. longo foliola parva minima ex parte squamiformia ut cetera pilosa et colorata gerente suffulta, densiflora, rhachi villosa; bracteae oblongo-lanceolateae, apice obtusae vel subacutae, brunnescentes, utrinque laxe longe sericeo-lanatae, circ. 3 mm. longae; stamina 2, filamentis liberis glabris bracteis duplo longioribus, antheris flavis ovali-ellipticis circ. 1.5 mm. longis; glandula 1, ovato-rectangularis, apice truncata, bractea circ. 3plo brevior.—Folia adulta in herb. Grayi ad no. 8047 addita elliptica vel subovato-elliptica, apice acuta, basi subrotundata, ad 11.5:4 cm. magna, superne laete flavo-viridia,

fere omnino glabra, subtus glaucescentia, pruinosa, glabra sed ad costam nervosque elevatos partim ferrugineo-pilosa, rete nervillarum perspicue elevato, textura papyracea; petioli villosuli 7–10 mm. longi.

TYPE LOCALITY.—Mexico: Federal District, Eslava and mountains west of the City of Mexico (female) and Serrania de Ajusco (male).

RANGE.—As above.

SPECIMENS EXAMINED.—Mexico: Federal District, Eslava, thickets, alt. 2300 m., April 14, 1904, *C. G. Pringle* (no. 13204, f.* type; W.; "15–20 ft."); mountain border west of the City of Mexico, April 26, 1849, *J. Gregg* (no. 680, f.; M.; "10 ft. high."); Serrania de Ajusco, alt. 2700 m., February 18, 1899, *C. G. Pringle* (no. 8047, m., paratype; G., M., W.; in Herb. N. mixed with fruiting *S. paradoxa;* in Herb. A. mixed with female var.? *cana* and a sterile branch which may belong to the male plant).

I am not fully convinced that the female and male plants really belong to the same species. The male plant may be the same as the female form called by me var.? *cana* below. Certainly, ROWLEE'S *S. cana* is not identical with the species of MARTENS and GALEOTTI. The description of these authors is rather incomplete, owing to the lack of fertile material, and I have not seen the type specimen. The statement "folia pollicaria," however, which probably refers to adult leaves, excludes a form like *S. Rowleei*, of which the leaves are much larger. Besides this the type of *S. cana* M. and G. has not been collected "in the same region" as the plant before us, the Peak of Orizaba being about 185 km. distant, as the crow flies, from the Cima de Ajusco. Furthermore, ROWLEE'S description does not apply exactly to all the specimens distributed under no. 6794 which ROWLEE cites as his type. The specimens in Herb. A., G., M., and W. consist only of female pieces which rather agree with the author's statement except (the base of the ovaries and) the pedicels being glabrous and not hairy. The male specimens which, I believe, belong to *S. Rowleei* are under *Pringle's* no. 8047 in Herb. G., M., and W.; while in Herb. N. the true male plant is mixed with a fruiting branch of *S. paradoxa* (see later), and in Herb. A. I find on the sheet of no. 8047 a male *S. Rowleei*, a female *S. Rowleei* var.? *cana*, a sterile branch which may belong to *S. Rowleei*, and a branch in winter condition. ROWLEE apparently describes male flowers of *S. paradoxa* or its var. *ajuscana* because he states that the filaments are hairy, while those of no. 8047 before me are glabrous. The male plant of ROWLEE therefore does not belong to *S. Rowleei* m. As to his female plant, there also remains some doubt about its identity, and those forms with a hairy pedicel (and a hairy base of the ovary) may possibly be of hybrid origin and represent a cross between *S. paradoxa*, var. *ajuscana* and typical *S. Rowleei*. After all, this species and the following variety need further observation in the field.

16b. S. ROWLEEI, var. (?) **cana** Schn., nov. var.—*S. cana* Rowlee, l. c., quoad plant. fem. sensu stricto, non Martens and Galeotti.—Habitus ramulique ut in *S. Rowleei* vel *S. paradoxa*. Folia adulta nondum visa, semievoluta textura colore et pubescentia ab iis *S. Rowleei* vix diversa, sed juvenilia magis (ut in *S. paradoxa*) ferrugineo-pubescentia, dein valde glabrescentia. Amenta fructifera ad 7:1.8 cm. magna, pedunculo ad 1 cm. longo foliola pauca parva normalia gerente suffulta, iis *S. Rowleei* satis similia (juvenilia non satis evoluta in ramulo ad no. 8046 in Herb. A. addito ad eandem formam pertinere videntur); flores fructusque iis *S. Rowleei* potius quam iis *S. paradoxae* similia sed pedicello et basi ovarii pilosa diversa.

TYPE LOCALITY.—Mexico: Federal District, La Cima de Ajusco.

RANGE.—As above.

SPECIMENS EXAMINED.—Mexico: Federal District, La Cima de Ajusco, alt. 3100 m., April 16, 1898, *C. G. Pringle* (no. 6794, fr., type; A., G., M.); same locality, alt. 2700 m., February 18, 1899, *C. G. Pringle* (no. 8047 quoad ramul. florif. femin. in Herb. A.).

See the remarks under typical *S. Rowleei* and under *S. paradoxa*.

17. **S. oxylepis** Schn., nom. nov.—*S. latifolia* Mart. and Gal. in Bull. Acad. R. Brux. **10**[1]:344 (Enum. Pl. Gal. Mex. 4). 1843, non Forbes 1828; Hemsley in Biol. Centr. Am. Bot. **3**:180. 1883.—Habitus?; ramuli novelli annotinique floriferi dense griseo- vel subflavescenti-villosuli vel villoso-tomentelli, subangulati (in no. 230 ramuli floriferi fusci satis glabrescentes), dein cinereo-fusci, glabrescentes. Gemmae bene evolutae non visae, puberulae. Folia tantum juvenilia visa, ovato-elliptica, vel obovato-oblonga, basi cuneata, apice breviter acuta (vel in no. 230 obtusiora), ad 4.5:1.5 cm. magna (in no. 230 ad 3:1.5 cm.), superne viridia, initio pl. m. laxe pubescentia, cito costa villosula excepta glabra, subtus discoloria, initio satis dense griseo- vel fulvo-villosa, dein glabrescentia, glaucescentia, pruinosa, costa nervisque prominentibus flavescentibus, rete nervillarum nondum distincte evoluto, margine subdenticulata (in no. 230 integerrima). Petioli pilosi, ad 4 mm. longi. Stipulae ut videtur minimae, caducae. Amenta subpraecocia vel coetanea, tantum mascula visa, cylindrica, ad 4.5:1.2 cm. magna (antheris delapsis tenuiora), subsessilia vel pedunculo foliola parva

pauca ut normalia villosa gerente ad 1 cm. longo suffulta, rhachi villosa. Bracteae elliptico-lanceolatae, acutae (vel in no. 230 anguste ovato-lanceolatae, subacuminatae), discolores, utrinque longe sericeae, ad 3 mm. longae; stamina 2, filamentis liberis vel ad basim $\frac{1}{6}$ coalitis circ. $\frac{1}{3}$ pilosis dein bracteam circ. $2\frac{1}{2}$plo superantibus valde elongatis, antheris flavis ellipticis; glandula 1, satis crasse et late rectangularis vel late ovato-rectangularis, apice truncata vel subemarginata, bractea circ. 3plo brevior.

TYPE LOCALITY.—Mexico: State of Puebla (or Vera Cruz) "sur les flancs du pic d'Orizaba, à 12000 pieds" [3700 m.] (coll. *Galeotti*, no. 70, ex Mart. and Gal.).

RANGE.—Central Mexico, on and near the Peak of Orizaba.

SPECIMENS EXAMINED.—Mexico: State of Puebla, Mt. Orizaba, alt. 2900–3200 m., March 18, 1894, *E. W. Nelson* (no. 272, m., type of *S. oxylepis* in Herb. W.); Boca del Monte [according to Rand MacNally's map 17 miles east of Esperanza], March 13, 1894, *E. W. Nelson* (no. 230, m.; W.).

S. latifolia Mart. and Gal. is a very little known species, of which the authors give a rather incomplete description of the male plant. Not having seen the type, I am not sure whether these specimens really belong to this species, but regarding the statement "squamis lineari-subulatis elongatis" and the fact that the type had been collected on the same mountain range, I believe that *Nelson's* plant may be identical with that of *Galeotti*. The name *latifolia* has to be changed on account of the earlier *latifolia* Forbes, which is a valid name. Owing to the incomplete material, it is impossible to decide whether *S. oxylepis* is a good species or perhaps only a variety of *S. paradoxa* Kth. s. l., to which those specimens belong that have been distributed as *S. latifolia* by PRINGLE. *Nelson's* specimens were named *S. lasiolepis*, var. *Bigelovi* by BEBB, but so far as I know this variety is entirely absent from Mexico.

18. S. PARADOXA Kunth in Humb. and Bonpl., Nov. Gen. Pl. **2**:20. 1817; Syn. Pl. Aequin. **1**:366. 1822; And. in DC. Prodr. **16**^{2}:226. 1868, in textu sub *S. discolore;* Hemsl. in Biol. Centr. Am. Bot. **3**:180. 1883.—Ad descriptionem auctoris incompletam addenda et emendanda: Arbor humilis densa, ad 6.5 m. alta; ramuli novelli ferrugineo-villosuli, pilis griseis intermixtis, hornotini paullo glabriores, annotini (floriferi) pl. m. tomentelli vel satis glabrescentes, atro-fusci, angulati. Gemmae (in no. 5698) ovato-oblongae, ventre planae, apice subrostratae, subadpressae, brunneae, paullo (saltem ad apicem) pilosae, ad 1 cm. longae. Folia (tantum in no. 5698 submatura) papyracea, oblongo-elliptica vel elliptico-

lanceolata, basi pleraque breviter cuneata, rarius subrotundata, apice acuta, minora inferiora (minimis basi ramulorum exceptis) 5:2 ad 8:2.5 cm. magna, majora superiora ad 13:3.5 cm. (vel ad 10:3.8 cm. in no. 1800 Purpusii) magna, superne tantum novella tomento ferrugineo cito evanescente obtecta, dein costa ferrugineo-tomentosa excepta fere glabra, viridia, subnitidula, nervis lateralibus distincte flavescentibus, etiam rete nervillarum subvisibili, subtus initio densius ferrugineo- vel subgriseo-tomentoso-villosula, cito costa nervisque prominentibus exceptis fere glabra, valde glaucescentia, pruinosa, reticulata, margine integerrima vel saltem versus apicem irregulariter et saepe indistincte glanduloso-subserrata. Petioli 3–13 mm. longi, superne subsulacti, undique ferrugineo-tomentelli. Stipulae cito deciduae, semiovatae vel semilanceolatae, parvae, ad 4 mm. longae, glanduloso-denticulatae, laxe piloase. Amenta praecocia vel subcoetanea, feminea tantum visa, crasse cylindrica, pedunculo brevi ad 1 cm. longo foliola parva lanceolata ut normalia pilosa gerente suffulta, florifera (in no. 1800) ad 6.5 cm. longa et 12 mm. crassa, divaricata, curvata, rhachi villosa; ovaria ovoideo-oblonga, pedicello iis circ. $\frac{2}{3}$ breviore incluso pl. m. dense villosa, stylo pedicello circ. $\frac{1}{3}$ breviore apice bifido coronata, stigmatibus oblongis angustis stylo subaequilongis vel sublongioribus bifidis; bracteae oblongae vel obovato-oblongae, obtusae, discolores, utrinque pl. m. longe albo-sericeo-lanatae, pedicello circ. $\frac{1}{3}$ longiores; glandula 1, ovato-rectangularis, apice truncata, pedicello subduplo vel subtriplo brevior; fructus ovoideo-lanceolati, subrostrati, pedicello circ. $\frac{3}{4}$ breviore incluso 8–9 mm. longi, ut ovaria vel minus dense villosi, valvis apertis satis recurvatis.

TYPE LOCALITY.—Mexico: State of Hidalgo, "prope Moran Mexicanorum, alt. 1330 hex." (coll. *Humboldt* and *Bonpland*, ex Kunth).

RANGE.—Central Mexico: probably from southern Hidalgo through Mexico, Federal District to Oaxaca.

SPECIMENS EXAMINED.—Mexico: State of Mexico, Ixtaccihuatl, alt. 2700–3200 m., December 1905, *C. A. Purpus* (no. 1800, f., fr.; G., M., N.).—Federal district, La Cima de Ajusco, April 18, 1900, *W. Trelease* (no. 135, fr.; M.; according to the large fruiting aments, the distinct styles, and the partly ferrugineous pubescence typical *paradoxa*).—State of Oaxaca, Sierra de San Felice, by springs, alt. 3200 m., May 18, 1906, *C. G. Pringle* (no. 10185, fr.;

"15–20 ft."); same locality, September 26, 1894, *C. G. Pringle* (no. 5698, st.; G.; leaves identical with those of the preceding no. in Herb. M.).

ANDERSSON says that he has seen of *S. paradoxa* nothing but "pauca specimina tantum eaque deformata." His statement "capsulae hirsutae longe pedicellatae, stylo nullo" does not apply to what I take for the typical *paradoxa*. KUNTH does not mention a style; he describes abnormal (androgynous) female aments, and according to his statement "amenta . . . . fructifera subtripollicaria, crassitie pollicis." I regard as *paradoxa* the plant with the very large fruiting catkins. This form has a distinct style which is very short (mostly hidden among the hairs of the apex of the ovary) in var. *ajuscana*, but this variety does not have "folia . . . . subtus nervo et venis primariis prominentibus ferrugineo-tomentosis" as KUNTH says, and the fruiting aments measure only up to 5:1.2 cm.

ROWLEE, in describing *S. Pringlei*, apparently mixed typical forms of *paradoxa* with those of var. *ajuscana*. Furthermore, he seems to have had before him another form with glabrous pedicels (see BOT. GAZ. **27**:137, *fig. 1, a–b*). I have not yet seen a specimen fully agreeing with ROWLEE'S description and figure, therefore I regard the true *S. Pringlei* as an obscure form not identical with *Pringle's* no. 6795 of the different herbaria I have seen. *S. Pringlei* may belong to a hybrid between *S. Rowleei* and *S. paradoxa* var. *ajuscana*, which both occur on the Cima de Ajusco.

18b. S. PARADOXA, var. **ajuscana** Schn., var. nov.—*S. Pringlei* Rowlee in BOT. GAZ. **27**:136. 1899, pro parte.—Frutex 0.5 ad 1.5 m. altus; ramuli novelli griseo-villosi, annotini floriferi fusco- vel olivaceo-brunnei, subangulati, parce (vel partim) villosuli vel subglabri, lenticellosi; gemmae bene evolutae nondum visae. Folia tantum semievoluta visa, elliptico-ovalia vel elliptica, apice acuta, interdum subplicata, base acuta vel subobtuse cuneata (vel minora subrotunda), majora 4–6.5:2–2.8 cm. magna (matura probabiliter satis majora), superne initio albo-pubescenti-villosa, dein viridia, costa nervisque lateralibus pl. m. exceptis glabrescentia (saltem in no. 13205), subtus dense albo-pubescenti-tomentosa, costa nervisque flavescentibus prominentibus, rete nervillarum sub pube occulto, glaucescentia, pruinosa, margine integerrima vel ad apicem obscure glanduloso-denticulata. Petioli ad 5 mm. longi, omnino villosuli; stipulae parvae semiovatae, denticulatae, villosulae, ad 3 mm. longae, caducae. Amenta praecocia, subsessilia, basi foliolis parvis squamuliformibus paucis subtus dense sericeis suffulta, rhachi villosa; mascula (in no. 6795) elliptico-cylindrica, ad 4 cm. longa et circ. 12–15 mm. crassa, vix curvata et divaricata; bracteae

discolores, anguste obovato-oblongae, apice rotundatae (interdum leviter eroso-denticulatae), utrinque longe lanato-pilosae; stamina 2, filamentis liberis dein bracteis subduplo longioribus basi $\frac{1}{3}$ villosis, antheris flavis ovoideis; glandula 1, elliptico-rectangularis, bractea 2–2$\frac{1}{2}$plo brevior, interdum satis lata. Amenta feminea florifera cylindrica 3–4:1 cm. magna, fructifera 4–5:1.5–1.7 cm. magna; ovaria ovoideo-oblonga, adultiora circ. 4 mm. longa et pedicello iis subduplo breviore suffulta (in floribus juvenilibus pedicellus quam glandula vix longior); stylus subnullus vel brevis, stigmatibus oblongis bifidis duplo brevior (vel in fructu stigmatibus subaequilingus). Fructus pedicello 3–4plo breviore incluso ad 7 mm. longi, dense villosi.

TYPE LOCALITY.—Central Mexico: Federal district, La Cima de Ajusco.

RANGE.—As above.

SPECIMENS EXAMINED.—Mexico: Federal District, La Cima de Ajusco, alt. 3200 m., April 16, May 21, 1898, *C. G. Pringle* (no. 6795, m., f., fr., type; G., M., W.; "2–5 ft."); same locality, April 16, 1904, *C. G. Pringle* (no. 13205, m., f., st.; G., W.; "2–3 ft."; M.; "dwarf"; forma ut videtur valde ad *S. paradoxam typicam* spectans).

ROWLEE cites *Pringle's* no. 6795 as type of his *S. Pringlei* and says "no staminate plant was collected," but the specimens before me consist of male and female material. Furthermore, ROWLEE states that the pubescence of the leaves is "slightly ferruginous" and that the leaves are "at maturity becoming nearly glabrous." As I have already pointed out, ROWLEE'S description does not fit exactly the material distributed under no. 6795, and I think it best not to use the name *Pringlei* for the variety because there may be hybrid forms. ROWLEE apparently overlooked the original description of *paradoxa*. He says that his species "is related to *S. candida*" which, in my opinion, has nothing whatever to do with the Mexican plant.

The var. *ajuscana* differs chiefly from *S. paradoxa* by its almost entirely grayish pubescence, the more elliptic or elliptic-ovate shape of the leaves, the shorter style of the ovaries, and the smaller size of the fruiting aments.

19. S. CANA Martens and Galeotti in Bull. Acad. Roy. Brux. 10[1]:344 (Enum. Pl. Gal. Mex. 4). 1843; Hemsley in Biol. Centr. Am. Bot. III:179. 1883.—Ramuli annotini tomento brevi denso cano vestiti, pl. m. angulati, dein subglabrescentes, atro-brunnei vel atro-purpurei; gemmae bene evolutae non visae. Folia adulta ignota, juvenilia anguste oblanceolata, basi subacuta, apice distinctius acuta et tenuiter mucronulata, 9:2 ad 18:4 mm. magna,

integerrima, superne viridia, ?nitidula, initio laxe sericeo-villosa, dein costa excepta glabrescentia, subtus discoloria, initio distincte partim brunnescenti-sericeo-villosa, dein ut videtur satis glabrescentia (et ? glaucescentia). Petioli brevissimi, ad 2 mm. longi, pilosuli. Stipulae non visae. Amenta mascula coetanea, minima, ovata, densiflora, ad 8:6 mm. magna, basi foliis iis longioribus obsita, rhachi villosula; bracteae obovato-oblongae, brunnescentes, apice rotundatae, utrinque satis laxe crispato-pubescentes; stamina 2, filamentis liberis bracteam ad 2plo superantibus basi $\frac{1}{3}$ villosulis, antheris flavis parvis elliptico-globosis; glandula 1, ovato-rectangularis, apice truncata, circ. $1\frac{1}{4}$ bracteae aequans.

TYPE LOCALITY.—Central Mexico: "habite les ravines humides du pic d'Orizaba, à environ 11 ou 12000 pieds d'élévation absolue" [3400–3700 m.] (coll. *H. Galeotti*, no. 69, ex. Mart. and Gal.).

RANGE.—Uncertain.

SPECIMENS EXAMINED.—Mexico: without exact locality, "Penas carg. April 1839," *C. Ehrenberg* (no. 1280, m.; W., ex Mus. Bot. Berol.).

The description of *cana* by the authors is very short and is based on sterile material only, and I have not yet been able to compare type material. It runs: "Canescenti-glauca; ramulis cinereo-subtomentosis, foliis subsessilibus oblongis integerrimis acutiusculis glabris subtus glaucis.—Amenta ignota, stipulae non visae, folia pollicaria.—Affinis *Salici paradoxa* H.B.K." By ROWLEE *Pringle's* no. 6794 had been regarded as *S. cana* M. and G., but, as I have explained under *S. Rowleii*, the plant from the Cima de Ajusco does not agree with the description of *S. cana*. This species of which the authors had apparently before them adult sterile specimens has "folia pollicaria." Considering the younger state, *Ehrenberg's* plant agrees well with the statements of MARTENS and GALEOTTI. Nevertheless, I am not yet sure about the identity of the two plants, especially as we do not know the exact habitat of *Ehrenberg's* plant. It has been referred to *S. cana* by such an eminent salicologist as v. SEEMEN according to the handwriting on the sheet.

There remains one more species described from Mexico:[17] *S. Endlichii* v. Seemen in Fedde, Rep. Spec. Nov. **5**:19. 1908. The type was collected by *R. Endlich* in the state of Chihuahua, "in

[17] There is also a *S. cinerea* Sesse and Moçino, Fl. Mex. ed. 2. 229. 1894, excl. syn., non L., described as "*Salix* foliis oblongis, denticulatis, subtus villoso-cinereis, stipulis semicordatis. F.M. Habitat in montibus umbrosis S. Angeli et plurimis Hisp. locis." There are 3 different localities bearing the name San Angel in Mexico. The description is much too incomplete to make even a guess at the identity of this obscure species.

den Thälern der westlichen Sierra Madre, 2250–2450 m. hoch," April 16–17, 1906 (no. 1225*a*, 1226). I have not seen any form from this state which agrees with v. SEEMEN's description, and unfortunately I have not been able to compare the type. Judging by the ample description, it seems to me that this species must be very similar to *S. cana* sensu meo. The narrow lanceolate leaves measure up to 1.6 cm. in length and 0.3 cm. in width; the aments are described as "coetanea, sessilia, basi foliis parvis obsita, parva, subglobosa, usque 0.7 cm. longa et lata"; and the fruits are "stipata (stipite capsulae dimidium aequante, dense incano-pubescente), e basi ovali conica, dense incano-pubescentia, stylus brevissimus, stigmata brevia emarginata capitellata; glandula 1 posterior, ovalis, truncata, capsulae stipitis dimidium aequans." After all, *S. Endlichii* may be a rather glabrescent form of *S. cana* or a closely allied species.

There are several Mexican specimens left which I believe may be regarded as of hybrid origin, or partly even as new species. At the present time I can only enumerate them, adding a few remarks. We need a much better understanding of the Mexican willows and more copious material of the forms in question before we can obtain a correct opinion of them.

(?) 1b×6. S. HUMBOLDTIANA, var. STIPULACEA×S. BONPLANDIANA.—State of Oaxaca, valle de Etla, alt. 1580 m., April 1906. *C. Conzatti* (no. 1722, fr.; W.).

It differs from the first in the smaller, more narrowly lanceolate subconcolorous leaves, which measure up to 10 by 1.2 cm. and possess numerous stomata in the upper epidermis. The branchlets are finely puberulent and dull reddish brown; the dense curved fruiting aments borne on short leafy peduncles (1 cm.) measure about 4 by 1 cm. The influence of *S. Bonplandiana* may be seen in the comparatively broader and firmer leaves with a pale under surface, and in the stouter aments. Possibly, however, it may be nothing but a form of var. *stipulacea*.

(?) 3×6. S. GOODDINGII×S. BONPLANDIANA (vel spec. nov. ?).—Southern Lower California: La Paz, January 20 to February 5, 1890, *E. Palmer* (no. 77, m.; W.); same locality, June 14, 1897, *J. N. Rose* (no. 1308, m.; W.).

The first specimen is named *S. Bonplandiana* var. *pallida*, the second *S. Bonplandiana*, but both do not represent the type or a form of this species

on account of the presence of stomata in the upper epidermis of the leaves. They look to me like hybrids between this species and *S. Gooddingii*, but I do not know whether the last species ever has been found so far south in Lower California. Instead of it one of the parents with stomata in the upper surface of the leaves may be *S. nigra* var. *Lindheimerii* (or even *S. Humboldtiana stipulacea*). The male flowers are very similar to those of *S. Bonplandiana*, the young branchlets and leaves are more or less pubescent (in no. 77 laxe subhirsuto-villosa), and the under surface of the (not yet mature) leaves is but slightly glaucous. Owing to the lack of female material, it is impossible to judge the form more correctly.

SALIX (?), spec. nov.—Territorio de Tepic, in the Sierra Madre, near Santa Teresa, August 11, 1897, *J. N. Rose* (st.; W.). These sterile branchlets seem to belong to a new species related to *S. Schaffnerii*, and may be described as follows: Ramuli hornotini apice pubescentia villosula griseo-brunnea vestiti, citissime glabrescentes et basim versus intense purpurascentes, glabri. Folia matura chartacea, anguste lanceolata, utrinque acuta vel apice subacuminata, minima 3:0.6 cm., maxima ad 9:1.2 cm. magna, dense glanduloso-subserrato-denticulata, superne initio sparse puberula, cito glabra, intense viridia, costa nervisque subflavescentibus, subtus albescentia, pruinosa, initio densius pilosa, dein fere glabra, costa nervisque elevatis et reticulata. Petioli vix 5 mm. longi, superne sulcati et pilosuli.

ARNOLD ARBORETUM

ALGAE OF THE HAWAIIAN ARCHIPELAGO. I

VAUGHAN MACCAUGHEY

The algae, particularly the seaweeds, of the Hawaiian Islands have attracted the attention of investigators for many years. In 1876 NORDSTEDT published a report upon the collections of BERGGREN ("De Algae aquae dulcis et de Characeis ex insulis Sandvicensibus a Sv. BERGGREN 1875 reportatis").

In 1881 a small list entitled "The algae of the Hawaiian Islands," by J. E. CHAMBERLAIN, appeared in THRUM'S *Hawaiian Almanac and Annual* for that year. In 1899 REINBOLD reported upon the collections of SCHAUINSLAND ("Meersealgen. Ergebnisse einer Reise nach dem Pacific; H. SCHAUINSLAND 1896–97." Abhandl. Naturw. Vereins Bremen 1899). The collector SCHAUINSLAND spent three months on the island of Laysan and made extensive collections of the algae of that island, of Oahu, and of the plankton between Oahu and Laysan. In 1901 Miss JOSEPHINE E. TILDEN published a popular article on "Algae collecting in the Hawaiian Islands" in *Postelsia*. This was an informal narrative of the visit made by herself and two other ladies to the islands in 1900. In 1902 Miss TILDEN published, in THRUM'S *Hawaiian Annual*, a list of 100 species entitled "Collection of algae from the Hawaiian Islands." In 1905 Miss MINNIE REED, science teacher at the Kamehameha Schools in Honolulu, published a valuable report in the *Annual Report of the Hawaii Agricultural Experiment Station*, entitled "The economic seaweeds of Hawaii and their food value."

In 1905 F. BRAND published "Anheftung der Cladophoraceen und über verschiedene polynesische Formen dieser Familie" (Beih. Bot. Centralbl. **18**:165–193). In 1905 E. LEMMERMANN published a very comprehensive paper ("Die Algenflora der Sandwich-Inseln," Bot. Jahrb. **35**:607–663), including plankton studies, and full records of the collections of SCHAUINSLAND.

In 1905 W. A. SETCHELL, who had made a short visit to the islands, published a paper on "Limu" (the Hawaiian word for seaweeds) in Univ. Cal. Pub. Bot. **2**:91–113. In 1910 Miss

TILDEN, in her "Minnesota algae, vol. I. Myxophyceae of North America," etc., included all available records of Hawaiian species and their distribution. In 1911 F. K. BUTTERS published "Notes on the species of *Liagora* and *Galaxaura* of the central Pacific" (Minn. Bot. Studies 4:161–184). In 1917 the writer published a paper on "The seaweeds of Hawaii" (Amer. Jour. Bot. 8:474–479. 1916).

The present paper is an effort to coordinate in a somewhat comprehensive and systematic form the scattered researches of nearly half a century, and to emphasize the ecological aspects of the Hawaiian algae. During a residence of 10 years in the islands the author has had opportunity to visit all of the larger islands, and to study the various algae habitats, from dredging operations along the reefs at a depth of 20 fathoms, up to the highest summits in the archipelago (nearly 14,000 ft.). His studies are incorporated in the present paper, but liberal use has been made of the investigations of others, particularly those of TILDEN, REED, and LEMMERMANN, to whom full credit is given for their pioneer labors.

Coral reefs

Because of their conspicuous situation along the coral reefs, large size, and economic value to the natives, the algae of the marine benthos flora have attracted particular attention. Seventy-five species, representing at least 40 genera, were habitually used for food by the ancient Hawaiians, and for these the natives had distinctive names.

Notwithstanding the relatively rich alga flora of the coral reefs, SCHIMPER's statement that "in opposition to the terrestrial tropical marine vegetation is less luxuriant and apparently less rich in forms than is that of the temperate and polar regions" holds true for the Hawaiian Islands. Moreover, the rockweeds, kelps, and laminarias that dominate the coasts of the cold countries are conspicuously absent from the Hawaiian flora. The distribution of the Hawaiian marine algae is intimately associated with the coastal topography and the development of the coral reefs and shallows. The older islands of the group, which are also the lowest, owing to the combined action of erosion and subsidence, have the

most extensive coral reefs. At the other extreme stands Hawaii, the youngest, highest, and largest island in the archipelago, with practically no lowlands or coral beaches, and very little reef coral.

The oldest islands of the series are the tiny reefs and shoals dotted along an axis 1800 miles long, lying to the west of the main group. Although of little commercial value, and with a combined area of only 6 square miles, these little islands are of great interest from the standpoint of their alga flora. Nihoa, French Frigates Shoal, and Gardner are eroded volcanic blocks, 170–900 ft. high, rimmed with fringing coral. Laysan and Lisianski are elevated coral islands, 45–55 ft., with fringing reef. Pearl and Hermes, Midway, and Ocean are typical coral atolls. Maro and Dowsett's reefs have visible surf, but no exposed coral. The entire series, named in sequence from east to west, is Nihoa, Necker, French Frigates Shoal, Gardner, Dowsett's Reef, Maro Reef, Laysan, Lisianski, Pearl and Hermes Reef, Midway, Ocean. SCHAUINSLAND[1] spent three months on Laysan and made extensive collections of the marine flora, both plankton and larger forms, but no thorough explorations have been made of the algae on the other isles and reefs.[2] When such an exploration, or series of explorations, is made, there is not the slightest doubt that a large number of new forms will be revealed, and that very important contributions will be made to the algology of the Central Pacific region. The significant feature of this long chain of tiny islets is that it undoubtedly represents the various stages in the subsidence of a titanic submarine mountain chain.

Some of the representative forms collected by SCHAUINSLAND at Laysan, and therefore to be expected along the shores and in the lagoons of others of these westward isles, are *Chondrocystis Schaunslandii*, *Gomphospharia aponina*, *Coleosphaeriopsis halophila*, *Xenococcus laysanensis*, *Oscillatoria bonnemaisonii*, *Spirulina subtilissima*, *Phormidium laysanense*, *Lyngbya mucicola*, *L. meneghiniana*, *Aulosira Schaunslandii*, *Caulerpa pinnata*, *Stypopodium lobatum*, *and Liagora coarctata*.

[1] SCHAUINSLAND, H. H., Drei Monate auf einer Korallen Inseln. Bremen. 1899.

[2] MACCAUGHEY, VAUGHAN, The little end of Hawaii. Jour. Geog. 15:23–26. 1916; also Outstanding biological features of the Hawaiian Archipelago, in press.

KAUAI AND OAHU

Of the larger eastward islands, Kauai and Oahu are of particular note, as they have the largest coral reefs and support the most luxuriant marine flora. The reefs are all of the fringing and platform types, and vary in width from a few hundred feet to half a mile. Reefs are well developed along the southern or leeward shores of the two islands, and also, to a less degree, along the northern coasts. Oahu is practically encircled by coral, whereas Kauai has numerous coastal stretches entirely free from coral. The little island of Niihau, to the west of Kauai, has considerable coral reef. There are a number of regions along the Oahu coast which are especially favorable for collecting marine algae and for the study of their ecology. These are (1) the Waikiki region, between Honolulu Harbor and Diamond Head; (2) the Pearl Harbor region; (3) the Coral Plain and reef south of Ewa, between Pearl Harbor and Barber's Point; (4) the Waianae coast, which has extensive and well protected reefs; (5) the Wai-alua coast, which is not as well protected as that of Waianae; (6) the Kahuku region, with large sandy beaches and shoals; (7) the Ka-hana region, with drowned valleys and crescentic beaches; (8) Kane-ohe Bay, a beautiful body of water, 8 miles long and 3 miles wide, filled with coral islands and shoals; (9) Kai-lua and Wai-manalo, with lovely coral beaches and reefs; (10) the Koko Head and Mauna Loa district, with broad reef platforms half a mile wide. Most of the collecting by visiting algologists (TILDEN, SCHAUINSLAND, BERGGREN, etc.) was done along the Waikiki reefs, and also at Waianae. It has been the privilege of the author to visit repeatedly all of the reefs enumerated.

The following popular account[3] of a visit to a coral reef will serve to indicate the general features of this interesting life region.

> Arriving at a suitable location, where the water was only two or three feet deep, we anchored the canoe and prepared for wading. We were equipped with old shoes to protect our feet from the jagged, broken coral branches (which cause very painful and slow-healing wounds); with broad-rimmed hats to protect eyes, face, and neck from the intense glare of the sun and water;

[3] MACCAUGHEY, VAUGHAN, Coral reefs of the Hawaiian Islands. Jour. Geog. 14:252–255. 1916; also A survey of the Hawaiian coral reefs, in press.

with geological hammers for breaking off fragments of coral; and with sundry haversacks, bottles, wide-mouth vials, etc. With our water boxes as guides we wandered for three delightful hours over the ledges, knolls, and sandy pockets of the reef; collecting, exploring, and rejoicing in the luxuriant abundance of marine life of every form and color. Branches of living coral; many kinds of curiously shaped shells; bright spotted crabs and crustaceans of various sizes; spiny sea-urchins; spidery-armed brittle-stars; exquisitely beautiful hydroid colonies; purple and black sea-cucumbers; delicate marine algae of many genera, reds, browns, olives, and greens of varying tints, a kaleidoscopic succession of queer marine organisms.

ECOLOGICAL ZONES ON REEF

The typical fringing reef exhibits 5 distinct zones or areas of plant and animal life. This zonation is best developed on the reefs with wide lagoons and a well defined outer margin or rim.

1. *Beach or inshore waters.*—The shallow inshore waters, varying in depth from 6 to 36 inches, sustain a number of the quiet water forms, such as *Enteromorpha* spp., *Hypnea nidifica*, *Gracilaria coronopifolia*, *Chaetomorpha antennina*, *Ulva* spp., *Chondria* spp., *Liagora decussata*, etc. The bottom is of coral sand or mud, more or less contaminated with volcanic wash from the mountains. The nature of the bottom depends upon the proximity of streams and the strength of the surf. In many places (Kai-lua, Mo-kapu, Mana) the bottom is pure white coral sand, with practically no mud or rock. In other districts (Kalihi, Nu'u-anu, Kane-ohe) there are large "mud flats" exposed at low tide, and the bottom here is very muddy and rocky, with little sand. Every gradation may be found between these two extremes. At the mouths of streams, and at other places along the coasts where fresh water springs exist below the tide level, the inshore water is sufficiently brackish to prohibit the development of the strictly marine species.

2. *Partially submerged rocks.*—In some places the beach and shallow waters are devoid of rock masses, but as a general condition one finds partially submerged rocks scattered all along the coasts. These may be either close inshore, in the form of ledges or little cliffs, or may lie at varying distances from the shore. In any case they distinctly indicate, by their horizontal bandings of algal and hydroid life, the ranges of high and low tide. These rock masses

are either of consolidated reef coral or of black basaltic lava. Some algal species show a preference for the coral (*Sargassum*, *Gracilaria*, *Laurencia*), others for the lava blocks (*Gelidium*, *Ahnfeldtia*, etc.). The rocks may be in somewhat protected situations, or may be exposed to the full force of the surf. The alga flora will depend largely upon the situation of the rocks with reference to the surf. The following kinds occur on rocks which are exposed to the continual battering of the surf: *Gymnogrongus* spp., *Asparagopsis Sanfordiana*, *Codium* spp., *Sargassum* spp., *Dictyota acutiloba*, *Haliseris plagiogramma*, *Gelidium* spp., *Ahnfeldtia concinna*, *Porphyra leucosticta*. The controlling factor in the alga flora of the partially submerged rocks seems to be the circulation of pure, well oxygenated sea water. Rocks in stagnant or impure water support a scanty flora as compared with those in surf-swept localities.

3. *Pools*.—Passing out beyond the rock litter we come to a zone characterized by numerous pools or pockets. These cuplike depressions in the lagoon floor vary in size from little pockets a meter in depth and diameter to large pools 5–10 m. in depth and diameter. The pools are easily distinguished by the darker tint of their waters as contrasted with that of the shallow lagoon. These pools in the floor of the lagoon are not to be confused with the "tidal pools" along the beaches. The lagoon pools are inhabited by a variety of algae and animals that prefer these shadowy havens to the exposure of the shallows or the outer reef. The bottom of the pool may be covered with clear coral sand, or coral débris, or masses of growing coral; its alga flora will depend upon its depth and the resultant intensity of illumination.

The following are typical forms that inhabit the lagoon pools: *Lithothamnion* spp., *Corallina* spp., *Peyssonnelia rubra*, *Grateloupia filicina*, *Ceramium clavulatum*, *Amansia glomerata*, *Polysiphonia* spp., *Chondria tenuissima*, *Laurencia* spp., *Martensia flabelliformis*, *Champia compressa*, *Wrangelia penicillata*, *Galaxaura lapidescens*, *Padina pavonia*, *Sphacelaria furcigera*, *Hydroclathrus cancellatus*.

4. *Lagoon*.—The entire region between the beach line or strand and the seaward rim of the reef is properly the lagoon, but for the purposes of this paper the term will be restricted to the deeper waters, which usually lie about midway between the beach and the

reef rim. As one approaches the lagoon, wading is no longer possible, the water is 3–10 m. or more deep, but again becomes shallower as the outer edge of the reef is reached. The water of the lagoon is placid, clear, and very transparent, so that the bottom receives good illumination. Although a number of the smaller algae grow upon the floor of the lagoon, the region is comparatively barren as compared with the shallower waters on either side. The lagoon floor is a region of coralline and animal life, rather than of the larger plant life. The quantities of sand that are constantly washed over the floor from the disintegrating reef rim render it difficult for plants to maintain themselves. Probably if conditions for collecting on the lagoon floor were more favorable, a larger number of species would be found than are apparently present.

5. *Reef rim.*—Upon rowing across the lagoon to the outer rim of the reef, one comes to shallow water, where the surf breaks, and where wading is possible. This zone is a favorite fishing ground of the native Hawaiians, and it abounds with both animal and plant life. The highest portions of the rim may be practically exposed at low tide, although at high tide they will be covered by 18–24 inches of water. The rim of the reef is by no means regular or symmetrical; there are many indentations, crags, débris slopes, pools, hummocks, and sandy spots all along the outer margin. Almost all of the visible coral in this region is living coral, associated with an abundance of corallines, bryozoans, hydroids, red algae, and other forms of life. Some of the algae that are confined largely to the outer reef rim are *Haliseris*, *Dictyota*, *Codium*, *Asparagopsis*, *Gymnogongrus*, *Porphyra*, *Turbinaria*, *Gelidium*, etc. Many of the species that inhabit these surf-churned waters are not the tough, cartilaginous forms, but very delicate and fragile species, that apparently survive the wave action because of their very delicacy. This is particularly true of some of the finer red algae.

TIDES

The situation of the Hawaiian Islands, in the great stretches of the North Pacific, is such that the tides are very small; in contrast with the tides usual along continental coasts they are exceedingly small. The average rise and fall lies within a vertical range

of 18–24 inches. The difference between high and low tide is so small that there is almost a complete absence of the strongly developed tidal zonation so characteristic of many continental shores. However, on the broad platform reefs, like those near Pearl Harbor, Waialae, and Mauna-lua, this difference is sufficient to expose much of the reef surface at low tide. At this time the reef consists of an irregular series of pools, cut off from one another by the rocky platform, which has only 2–3 inches of water on it. Protruding areas of the reef are wholly exposed to the air, and on their knobs or knolls only the hardy species of algae can exist. Out toward the edge of the reef a shallow lagoon, or series of lagoons, may persist, unemptied by the lowest tides. This is the ideal time for collecting, as one can travel afoot far out to the rim of the reef and easily procure material which at high tide is hidden beneath the surf and foam. To get the full advantage of the low tide one customarily begins work when the tide is about half run out, and then follows the ebb out to its maximum. This gives a working period of 4–5 hours.

CORALLINE ALGAE

Highly important among the Hawaiian marine algae are the coralline or "stony" algae or nullipores. A number of genera (*Lithothamnion*, *Corallina*, *Mastophora*, and others) are abundant on the Hawaiian reefs, and have undoubtedly been highly effective in reef building. The importance of these lime-secreting algae was overlooked by the earlier students of the coral reefs, but is now beginning to receive adequate consideration. As MAYER[4] states:

> The most striking feature which distinguishes the Pacific reefs is the development of a ridge which actually projects half a foot or more above low tide level and extends along the outer seaward edge of the reef-wall wherever the breakers dash. In the Paumotus this ridge is dull reddish pink in color, and it is composed of a mass of stony seaweeds or nullipores of the sort called *Lithothamnion*, and also of bryozoa which are remarkable lime-secreting organisms related more closely to the worms than to any other form of the animal kingdom.
>
> This *Lithothamnion* ridge thrives only where the breakers strike in full force upon its living barrier, and it serves as the chief protector of the island, breaking the force of every wave that approaches the windward shore.

[4] Popular Science Monthly **85**: 209–231. 1914.

HOWE,[5] in a digest of our present knowledge of the lime-secreting algae as reef makers, shows that in the famous boring at Funafuti, which was driven to a depth of 114.5 ft., *Lithothamnion* was found to be more or less abundant through the entire length of the boring; *Halimeda* was locally very abundant from 28 to 1096 ft. According to the same paper *Lithothamnion* is now recognized to be a dominant reef builder in the reefs of Fiji, Gilberts, Dutch East Indies, Bermudas, and other groups.[6] He states that the lime-secreting seaweeds flourish and are effective reef builders in greater depths than is the case with corals. There are numerous records of these forms at depths of 100 fathoms, *in situ*, and occasionally at 250–350 fathoms, whereas 25–40 fathoms is the greatest depth attained by the reef-building corals. HOWE continues:

> Besides flourishing in greater depths than the corals, the lime-secreting seaweeds are much less dependent upon high temperatures than are the corals. . . . . The coralline algae are, locally at least, abundant from 73°5′ south latitude to 79°56′ north latitude. . . . . He specifies the seas off the coasts of Spitzenberg, Nova Zembla, Iceland, Greenland, and Norway, where banks of *Lithothamnion* cover the bottom for areas of many square miles. . . . . The massive beds of *Halimeda opuntia* off the Florida Keys (the same species . . . . that is filling the lagoons of some of the South Sea atolls) are striking, as are the banks of *Goniolithon strictum* in the Bahamas, and reefs of *Lithophyllum antillarum* and *L. daedaleum* along the shores of Porto Rico. . . . . The lime-secreting plants appear to be much more generally and widely distributed, both horizontally and vertically, than are the corals.

The Hawaiian corallines inhabit the shallow waters, as well as occurring at considerable depths. In the former situations they form beautiful rose, purple, and lavender incrustations. On the faces of cliffs that are washed by the sea the incrustation appears as a conspicuous rose or purple band, extending from high tide mark or the uppermost wash of the surf, down to the zone of minimum illumination. The lower margin of the coralline zone has not been investigated in the Hawaiian Islands, but it undoubtedly reaches as great depths as in the island groups already cited. The upper margin is often somewhat above high tide mark, as these

[5] HOWE, M. A., Building of coral reefs. Science, N.S. **35**:837–842. 1912.

[6] See also SEWARD, A. C., Algae as rock-building organisms. Science Progress **2**:10–26. 1894.

algae are able to live even if they receive only intermittent spray wash. In this coralline zone are many of the calcareous hydrozoa.

TIDAL POOLS

Along the rocky coasts, where there are extensive shelves or ledges of lava or uplifted coral limestone, tidal pools are of common occurrence. The pools that lie nearest the water line are filled at every tide; indeed, many lose their identity as pools at each tide. Those at higher levels, and farther from the water line, may be filled only at times of very heavy surf, and dry up for considerable intervals. These variable conditions greatly affect the alga flora. The pools vary in size from mere puddles to large basins 10–20 m. long and 3–5 m. in depth. These large perennial basins support an alga flora very similar to that of the shallow lagoon waters. Excellent examples of tidal pools occur along the southern coast of Kauai, the Maka-pu'u region of Oahu, the north coast of Molokai and Maui, and along the Kona coast of Hawaii. Some of the algae common in the ordinary tidal pools are species of *Limnothamnion*, *Wrangelia*, *Liagora*, *Padina*, *Ectocarpus*, *Sphacelaria*, *Halimeda*, *Caulerpa*, *Cladaphora*, *Chaetomorpha*, *Enteromorpha*, *Monostroma*, *Calothrix*, *Scytonema*, *Hormothamnion*, *Hydrocoleus*, *Lyngbya*, *Phormidium*, *Oscillatoria*, etc.

CORAL REEFS ON OTHER ISLANDS

Special mention has been made of the reefs of Kauai and Oahu. The islands of Molokai, Maui, Lanai, and Ka-hoo-lawe all possess some coral reefs, but nowhere is the development of the alga flora as great as upon Oahu. The island of Molokai, both windward and leeward sides, ranks first among the 4 islands enumerated. The island of Hawaii, with an area larger than the combined area of all the other islands, is the poorest in marine algae. In fresh water species, however, it takes precedence over several of the smaller islands. The coasts of Hawaii are rugged and precipitous, and the deep offshore waters are not favorable for algae.

Taro loi and rice fields

Turning now to the habitats of the fresh water flora, we consider first the taro loi. The Hawaiians and Chinese raise the taro plant

(*Colocasia esculenta*) in irrigated patches called "loi." These are located on the lowlands and valley floors. Water is skilfully diverted from the mountain streams, and spread in a thin sheet over the loi. These tiny fields are each only a fraction of an acre in area, and many are only 20–30 ft. each way. The bottoms and low retaining embankments are composed of black volcanic alluvium. The loi are not continuously under water, but are flooded only at certain stages in the development of the taro. In this way each loi is at one time a shallow pond 6–12 inches in depth, at another a sheet of very soft, water saturated mud, and at another a sheet of fairly compact mud. These loi are notable habitats for the various fresh water algae, which occur in great variety and luxuriance. The algae may be found, according to their specific habitats, either floating on the surface of the water, free swimming in the water, growing upon the muddy bottom, epiphytic upon the stems of aquatic plants, or growing along the moist margins of the embankments, near the water's edge.

In recent years many of the taro patches have been converted into rice fields by the Chinese. The general conditions of irrigation, so far as influencing the alga flora are concerned, are practically the same for the rice as for the taro. Luxuriant growths of many fresh water species may be found in the rice fields. Some of the representative species occurring in these situations are as follows:

FLOATING AND FREE SWIMMING.—*Chroococcus*, *Raphidium*, *Scenedesmus*, *Gloeothece*, *Aphanothece*, *Merismopodium*, *Xenococcus*, *Lyngbya*, *Anabaena*, *Scytonema*, *Hydrodictyon*, *Conferva*, *Ulothrix*, *Cladophora*, *Spirogyra*, etc.

EPIPHYTIC.—*Chamaesiphon*, *Lyngbya*, *Coleochaete*, etc.

ON BOTTOM OR MARGIN.—*Lyngbya*, *Nostoc*, *Anabaena*, *Scytonema*, *Stigonema*, *Calothrix*, *Rivularia*, *Gobium*, *Draparnaldia*, *Oedogonium*, *Bulbochaete*, *Nitella*, *Chara*, *Mougeotia*, *Zygnema*, etc.

Ditches and flumes

A habitat for many kinds of algae is the irrigation ditch or flume. The very general use in the islands of irrigation water for the raising of taro, rice, sugar cane, and other crops has led to the development of elaborate systems of ditches and flumes. The inner walls and margins of these water channels support a diversified algal flora, despite the intermittent nature of the water supply. Many of the flumes are constructed of rough wooden planking,

which often has sufficient leakage to stimulate extensive algal growths, either pendent from the under side of the flume or in the drip zone beneath it. Genera that are of frequent occurrence in the ditches and flumes are *Gloeocapsa, Aphanothece, Oscillatoria, Spirulina, Phormidium, Lyngbya, Nostoc, Anabaena, Cylindrospermum, Scytonema, Tolypothrix, Ulothrix, Stigeoclonium, Nitella, Chara, Zygnema, Spirogyra,* etc.

Caves

There are many caves in the Hawaiian mountains. Some are of vast size, but the majority are relatively small. They occur at all elevations, from sea level to the highest summits, and are invariably due to volcanic activity in former times. Many contain pools of water; those at sea level frequently have salt or brackish water. The walls of the cave are usually moist, especially around the mouth, due to seepage from above. The conditions of continuous moisture and sufficient light, which prevail near the mouth of the cave, are favorable for the development of algae. Luxuriant growths, particularly of the Cyanophyceae, occur in these places. Representative species which inhabit these localities are *Gloeocapsa quaternata, Aphanothece Naegeli, Oscillatoria sancta, O. formosa, Spirulina major, Phormidium papyraceum, Nostoc* spp., *Anabaena variabilis, Scytonema varium, S. ocellatum, Fischerella ambigua, Characium minutum, Ulothrix minutula.*

Some typical Hawaiian caverns which support an abundant algal flora are those of Ha-ena, Kauai; Nu'u-anu, Manoa, and Maka-pu'u, Oahu; Kau-po region of Hale-a-ka-la, and Hana region, Maui; Hilo and Ka-u regions of Hawaii. Innumerable smaller caverns are scattered throughout the mountainous regions of all the islands.

Mountain streams

The rainfall on the upper slopes (2500–6000 ft.) of the Hawaiian mountains is torrential. This has carved deep valleys, penetrating into the heart of the mountains. These valleys vary in length from a mile to 10–12 miles. In width they range from narrow, rock-walled, sunless gorges to great amphitheaters, several miles in diameter, and rimmed by tremendous precipices. In the floor of each valley is a narrow stream, rarely more than 12 ft. in width.

The slope of most the valleys is so steep, and the drainage basin so restricted, that the run off is extremely rapid, and the fluctuations in stream volume are very pronounced. The upper course of the stream, through the rain forest, is littered with large lava boulders, dotted with small pools, and interrupted by numerous cascades. The waterfalls vary in height from a few feet to 1500 ft. These mountain streams, owing to their intermittent nature, are not very favorable for the algae, and luxuriant growth is rare. The contrast between the abundant algal flora of a flooded taro loi or rice field, on the warm lowlands, and the paucity of forms inhabiting a cold, intermittent mountain stream, is very striking. On the other hand, although the algae are not abundant, they are present in moderate quantities and in considerable diversity.

On the moist earth along the banks of the stream, on the rocks in the bed itself, and in the frequent pools one finds such algae as *Gleocapsa quaternata*, *Aphanothece Naegeli*, *Phormidium*, *Lyngbya*, *Anabaena*, *Scytonema rivulare*, *Tolypothrix distorta*, *Dactylococcus infusionum*, *Dictyosphaerium pulchellum*, *Raphidium polymorphum*, *Pediastrum*, *Conferva*, *Ulothrix*, *Stigeoclonium*, *Draparnaldia macrocladia*, *Oedogonium*, *Bulbochaete*, *Cladophora nitida*, *Nitella haviensis*, *Xenococcus Kerneri*, *Characium groenlandicum*, *Closteriopsis longissima*, *Schroederia setigera*, *Salpinocoeca minuta*, *Dinobryon sertularia*, *Hemidinium nasatum*, *Asterionella formosa*, *Triploceros*, *Melosira*, *Cyclotella*, *Cymatopleura*, etc. The faces of the waterfalls, and the dripping cliffs immediately adjacent, are the habitats of such forms as *Gloeocapsa magma*, *Oscillatoria* spp., *Spirulina major*, *Nostoc* spp., *Scytonema varium*, etc.

Hot springs and thermal waters

The only waters in the Hawaiian Archipelago that have temperatures higher than that of the atmosphere are those in the vicinity of the active volcano Kilauea, Hawaii. There are a number of warm pools and springs in the Puna district, and these evidently all receive their heat from the subterranean molten lavas of Kilauea. The temperatures of these waters vary between 30 and 35° C. These warm pools contain a luxuriant algal growth, especially in the form of a coating over the rocks that form the sides and floors of the pools. Representative thermal species are *Fischerella thermalis*,

Gloeocapsa thermalis, Haematococcus thermalis, Microcoleus paludosus, Plectonema nostocarum, Schizothrix havaiensis, Scytonema azureum.

Summit bogs

A type of habitat differing markedly from those that have been described are the five bogs which occur on the summits of Waiale-ale, Kauai, Ka-ala on Oahu, East Molokai, West Maui, and the Kohala Mountains of Hawaii.[7] These bogs lie at an elevation of 4000–6000 ft., in a zone of almost continuous cloud and rain. The annual precipitation in these regions amounts to several hundred inches, perhaps as high as 500. The soil is perpetually saturated, and is covered with a blanket of alpine sedges, rushes, grasses, mosses, and liverworts. In this substratum, and in the relatively small and infrequent pools that occur here and there on the surface of the bog, there is a considerable variety of algae. It is to be regretted that the alga flora of the summit bogs has not received careful investigation. The higher plants that inhabit these regions are mostly endemic species and varieties, and it is probable that a proportion of the algae would also prove to be endemics. The blue-greens are the dominant group.

Brackish waters

At various places along the coasts, but particularly where the larger streams empty into the sea, are areas of brackish water. These may be either the actual mouth of the stream itself, lagoons, or swamp lands. In any case, these waters are inhabited by species which differ both from the strictly fresh water forms on the one hand and the marine species on the other. Many of the brackish water forms are used by the Hawaiians as food. Typical forms of these waters are *Enteromorpha* spp., *Oedogonium obsoletum*, *Chaetomorpha pacifica*, *Cladaphora* spp., *Nitella havaiensis*, etc.

Halophytes

LEMMERMANN lists a few halophytes from the "Salt Lake" Crater of Moana-lua,[8] and from the Laysan lagoon, which is about

[7] MACCAUGHEY, VAUGHAN, Vegetation of the Hawaiian summit bogs. Amer. Bot. 22:45–52. 1916.

[8] This is no longer highly saline, as an artesian well has been bored in its bottom, and the lake converted into a fish pond.

three times as salty as sea water. The species are *Amphora ovalis* var. *pediculis*, *Lyngbya mucicola*, *Nitzschia angularis*, and *Coleosphaeropsis halophila*. The Laysan lagoon is the only known place in the archipelago possessing water of greater salinity than that of the sea, although of course the evanescent tidal pools attain a high degree of salinity in their later stages.

Fish ponds

Many of the free floating and filamentous algae are very abundant in the "loko" or fish ponds. These are shallow waters along the coasts that have been cut off from the open sea by means of heavy stone walls. The wall usually extends out from the land in the form of a crescent, pierced here and there by grated openings or gates, which permit the passage of the tides and very small fish, but which effectually retain the larger fish. The water within the pond is not disturbed by the surf, and the life conditions are more tranquil than those of the lagoon or sea. In ancient times some of the loko were utilized by the Hawaiians for a crude kind of limu culture. *Enteromorpha* and other coarse filamentous forms often form extensive floating mats on the waters of the loko. These ponds are most numerous on the islands of Oahu and Molokai, and have a combined area of many hundreds of acres.

Phytoplankton

The author has made no studies of the Hawaiian phytoplankton and so can only summarize here the extensive studies of SCHAUINSLAND and LEMMERMANN. The totals given by the latter authority are as follows:

	In Pearl Harbor	Between Hawaii and Laysan	Open Roadstead at Laysan
Schizophyceae	0	7	0
Chlorophyceae	0	2	0
Silicoflagellatae	0	3	0
Peridiniales	11	29	4
Bacillariales	11	10	12
Totals	22	51	16

The number of species of the last two groups, excluding duplicates, was 33 Peridiniales and 31 Bacillariales. The Hawaiian waters await an exhaustive study of their plankton; such a study will undoubtedly bring to light much new material of great interest.

Deep water forms

There have been no large investigations of deep water forms in the vicinity of Hawaiian waters comparable to those made in other parts of the ocean. The Hawaiian Islands all slope off very abruptly into deep water. There is little evidence of shelves or platforms. The outer faces of the coral reefs are all very precipitous, in striking contrast with the gentle slope of the inner or lagoon face. By some geologists the islands have been compared to the summits of a row of obelisks. The inter-island channels are very deep. The following table will make clear the extensiveness of the deep waters in the immediate vicinity of the islands:

Channel between Kauai and Oahu			1872	fathoms or	11,232 ft.
"	"	Oahu and Molokai	384	"	2304 "
"	"	Molokai and Maui	135	"	810 "
"	"	Maui and Hawaii	1032	"	9192 "

Endemism

The endemism which is so striking a feature of the terrestrial flora is exhibited to only a very minor degree by the algae. It is difficult to make any very comprehensive statement on this subject, as our knowledge of the algal flora of other Pacific Islands is still very incomplete. The following are typical forms which may be considered endemic in the present status of our knowledge: *Corallina sandwicensis*, *Mastophora tenuis*, *Laurencia nidifica*, *Plocamium sandwicense*, *Sargassum obtusifolium*, *S. polyphyllum*, *S. densum*, *S. incisum*, *Zygnema spontaneum*, *Oedogonium globosum*, *Draparnaldia macrocladia*, *Conferva sandwicensis*. Most of the algae are either cosmopolitan species or else widely distributed in many tropical and subtropical waters.

COLLEGE OF HAWAII
HONOLULU

WESTERN PLANT STUDIES. V

ÅVEN NELSON AND J. FRANCIS MACBRIDE

SISYRINCHIUM IDAHOENSE Bickn., var. **birameum** (Piper), n. comb.—*S. birameum* Piper Contrib. Nat. Herb. **11**:203. 1906.—This variety may be distinguished ordinarily by the presence on the plant of one or more branched stems. Professor J. K. HENRY of Vancouver has kindly sent us specimens of the species transitional to the variety. These are deposited in the Gray Herbarium under his no. 9056 and were secured June 27, 1916, near Alberni, Vancouver Island. He wrote regarding them "all growing together and sometimes in the same bunch."

Sisyrinchium boreale (Bickn.), n. comb.—*Hydastylus borealis* Bickn. Bull. Torr. Bot. Club **27**:378. 1900.—BICKNELL was surely justified in segregating this small-flowered inhabitant of inland lakes from the truly maritime large-flowered *S. californicum*. *H. brachypus* Bickn., *loc. cit.* 379, however, seems to be only a state of *S. californicum* that is unworthy any formal recognition.

Brodiaea coronaria (Salisb.), n. comb.—*Hookera coronaria* Salisb. Parad. Lond. *pl. 2.* 98. 1801; *B. grandiflora* Smith, Trans. Linn. Soc. **10**: *pl. 1.* 1811.—SMITH cites SALISBURY'S name as a synonym, and comparison of the plates shows that both authors had in mind the same plant.

Allium scissum, n. n.—*A. incisum* Nels. and Macbr. BOT. GAZ. **56**:470. 1913; not *A. incisum* Fomine in Monit. Jard. Bot. Tiflis **14**:52. 1909.

Trifolium Leibergii, n. sp.—Stems flexuous, 8–15 cm. high, 1–several from the summit of a woody taproot: petioles, leaves, and peduncles canescent with a dense covering of fine crinkly hairs: petioles 1–2.5 cm. long; leaflets obovate or subrotund, 1–1.5 cm. long, about 1 cm. broad, spinulose-serrate above the entire cuneate base: peduncles 1.5–2 cm. long; heads 1.5–2 cm. in diameter; flowers reflexed in age, distinctly pedicellate: calyx pubescent like the rest of the plant but the hairs longer and tangled; lobes linear-lanceolate, setaceous-acuminate at tip, nearly equal, thrice the

length of the tube, 3–4 mm. long: corolla purple; standard minutely crenulate at the rounded apex; tip of wings obtusish: pod pubescent like leaves; seeds 2.

This clover is most nearly related to *T. Lemmonii* Wats., but the remarkably long calyx teeth and the very different leaves and pubescence mark it as distinct. It is equally at variance, in these and other characters, with *T. gymnocarpon* Nutt. Miss McDERMOTT (N. Am. Trif. 194. 1910) regards *T. Lemmonii* as a variety of the latter. We are not certain as to the justification of this disposition, but these species are certainly more closely related to each other than to *T. Leibergii*. We have had the pleasure of designating many of LEIBERG'S specimens as types. It seems fitting, therefore, to call this unique clover *T. Leibergii*, based on his no. 2344 (as represented in the Gray Herbarium) from serpentine dykes near Dewey, Oregon, June 21, 1896.

CLARKIA

In a former contribution (BOT. GAZ. **61**:31–32. 1916) we expressed the opinion that the genera *Phaeostoma*, *Godetia*, and *Clarkia* should be united, because when all the species concerned are considered it is possible to establish an unbroken series on the same characters relied upon to maintain the genera as distinct. JEPSON in his careful revision of *Godetia* (Univ. Calif. Publ. Bot. **2**:319–320. 1907) pointed out its technical weakness and, after citing several standard works in which the genus is recognized, he wrote "in favor of its retention it may be urged that the genus forms a group of species which is very compact, that it does not include doubtful species, and that its ecological characteristics, habitats, time of flowering, and pollination devices are exceedingly uniform." In our judgment the only argument advanced here which will be affected in any way by the reduction of *Godetia* to *Clarkia* is the statement that "the genus forms a group of species which is very compact." This will not be truly applicable until in reality these genera *are* merged. As they now stand, it is impossible to "key out" certain species, even in ENGLER and PRANTL'S *Die natürlichen Pflanzenfamilien*, a work cited by JEPSON as an argument in favor of the maintenance of *Godetia*. When united with *Clarkia*, however, we have a genus which, considered in its entirety, represents as definite and distinctive a unit as there is in the family. JEPSON seems to have realized how unreliable and artificial the generic

bounds in this group are, but apparently felt our hesitancy (BOT. GAZ. **61**:32. 1916) in discarding the well known name *Godetia*. In a discussion (*loc. cit.* 352) of *G. delicata* Abrams,[1] he states, "on account of the clawed petals, hairy ring at orifice of calyx tube, and smoothish capsules, this species serves to emphasize in a marked manner the close relation between *Godetia* and *Clarkia*. It is most nearly allied to *Clarkia rhomboidea*." In this connection it is interesting to note that another species, *G. biloba*,[2] which is one of the connecting links between the genera (cf. JEPSON, *loc. cit.* 319, and NELSON and MACBRIDE, *loc. cit.* 32), has been found by Mrs. BRANDEGEE (JEPSON, *loc. cit.* 323) to have hybridized with *Clarkia elegans*.

It is unfortunate that JEPSON did not make his critical revision more inclusive. In the citation of specimens particularly he seems to have eliminated collections from the Northwest. This makes the determinations of material from north of California more difficult than it should be. PIPER and BEATTIE'S treatment in their recently published *Flora of the Northwest Coast* is helpful, but even it includes only 7 of the 13 species credited to the region. Accordingly it has seemed desirable in making the necessary transfers from *Godetia* to *Clarkia* to give, at the same time, a brief synopsis of the species.

Godetia tenella (Cav.) Steud. is not included; even the nature of the type seems to be very obscure (cf. JEPSON, *loc. cit.* 348). HOWELL'S *Fl. N. W. Am.* 235 contains *G. epilobioides* (Nutt.) Wats.[3] This distinctive species is confined to southern California (JEPSON, *loc. cit.* 343). Specimens so labeled from Oregon and Washington are usually referable to *G. gracilis* Piper. HOWELL does not include *G. grandiflora* Lindl.,[4] although the species was described from plants grown from supposedly Oregon seed. It seems to be known, however, only from the coastal region of central California. JEPSON (*loc. cit.* 348) reduces *Oenothera Whitneyi*

[1] **Clarkia delicata** (Abrams), n. comb.—*Godetia delicata* Abrams, Bull. Torr. Bot. Club **32**:539. 1905.

[2] **Clarkia biloba** (Durand), n. comb.—*Oenothera biloba* Durand, Pl. Pratt. 87. 1855; *Godetia biloba* (Durand) Wats. Bot. Cal. **1**:231. 1876.

[3] **Clarkia epilobioides** (Nutt.), n. comb.—*Oenothera epilobioides* Nutt. in T. and G. Fl. N. Am. **1**:511. 1840; *Godetia epilobioides* (Nutt.) Wats. Bot. Cal. **1**:231. 1876.

[4] **Clarkia superba,** n. n.—*Godetia grandiflora* Lindl. Bot. Reg. 27 Misc. 61. 1841, not *C. grandiflora* (F. and M.) Greene, Fl. Franciscana **2**:223. 1891.

Gray[5] to this species, but this is an error. LINDLEY's description of *G. grandiflora* reads "fructu lineari 4-sulcato tereti pubescenti." This description accords perfectly with the fruit of all collections we have seen. The capsules of GRAY's species, on the other hand, are far from linear, being thick and short, only 2 cm. long. JEPSON's description (*loc. cit.* 347, 348) of *G. grandiflora* applies rather to this species, and the specimens cited by him are referable here. In the following outline of the northwestern members of the genus *Clarkia* we have not cited specimens of the well known species.

Petals lobed, clawed.....1. *C. pulchella*
Petals entire or at least not lobed, sessile, or short clawed
  Stigmas linear; calyx lobes united and turned to one side in anthesis; capsules pedicelled or sessile
    Anthers 4–8 mm. long, more or less hooked or curved after dehiscence
      Buds usually erect; capsules sessile or subsessile, short beaked, teretish
        2. *C. amoena*
      Buds nodding; capsules long pedicelled and long beaked, 8-ribbed
        3. *C. arcuata*
    Anthers 3 mm. long, fertile to the tip, not becoming curved...4. *C. caurina*
  Stigmas short and broad; calyx lobes becoming free (except in no. 7); capsules sessile
    Capsules terete or nearly so and not prominently ribbed; flowers spicately scattered
      Leaves oblong to ovate.....5. *C. rhomboidea*
      Leaves linear
        Style only half as long as stamens; ovary densely white puberulent
          6. *C. Romanzovii*
        Style nearly as long as stamens; ovary slightly puberulent
          7. *C. gracilis*
    Capsules distinctly 4-sided or prominently ribbed; flowers (except in no. 8) in compact spikes or dense clusters
      Flowers scattered, the spikes usually long; petals 5–12 mm. long
        8. *C. quadrivulnera*
      Flowers in dense clusters or if not the petals much larger
        Stems erect, not flattened
          Capsules pubescent; petals 1–3.5 cm. long
            Style as long as or longer than the stamens; capsules puberulent
              9. *C. viminea*
            Style shorter than the long stamens; capsules usually shaggy-pubescent.....10. *C. purpurea*
          Capsules typically glabrous; petals less than 1.5 cm. long
            11. *C. Arnottii*
        Stems decumbent-ascending, flattened above.....12. *C. decumbens*

[5] **Clarkia Whitneyi** (Gray), n. comb.—*Oenothera Whitneyi* Gray, Proc. Amer. Acad. 7:340, 400. 1868.

1. CLARKIA PULCHELLA Pursh, Fl. 1:260. 1814.—It is not necessary to cite specimens of this beautiful and distinctive species. Its range is greater, however, than generally indicated in the books. Although most frequent from British Columbia to western Idaho and California, it crosses Montana and has been secured in the Black Hills of South Dakota. Often cultivated in the eastern states, it is of spasmodic occurrence there as a weed in newly seeded grounds, etc.

2. **Clarkia amoena** (Lehm.), n. comb.—*Oenothera amoena* Lehm. Ind. Sem. Hort. Hamb. 8. 1821.—This species and the next one are well marked by the character of the anthers curving after dehiscence. There is some variation in this, however, the cells sometimes being fertile to the tip and then tardily recoiling. Two noteworthy, but in themselves variable, color forms occur. These may be known as forma **concolor** (Jeps.), n. comb.—*Godetia amoena*, var. *concolor* Jeps. Fl. Mid. 334. 1901; and forma **Lindleyi** (Dougl.), n. comb.—*O. Lindleyi* Dougl. Hook. Bot. Mag. *pl. 2832*. 1828; *G. amoena*, var. *Lindleyi* Jeps. Univ. Cal. Publ. Bot. **2**:329. 1907. The latter is distinguished by the presence of a dark central blotch in the petals.

Coastal region, British Columbia to Monterey County, California.—OREGON: Willamette River below Portland, June 10, 1902, *Sheldon*, S. 10864; Calapooya Creek, Douglas County, July 24, 1899, *Barber* 75 and 76.—WASHINGTON: Tacoma, 1894, *Miss J. H. Van Rensselaer;* Sinclair's Inlet, Kitsap County, July 1895, *Piper;* near Chenowith, Skamania County, June 16, 1892, *Suksdorf* 2129; between Olympia and Gate City, Thurston County, July 15, 1898, *A. A.* and *E. Gertrude Heller* 4051 (form with anthers fertile to apex).

3. **Clarkia arcuata** (Kell.), n. comb.—*Oenothera arcuata* Kell. Proc. Cal. Acad. **1**:58. 1855; *Godetia hispidula* Wats. Proc. Am. Acad. **8**:599. 1873; *G. arcuata* (Kell.) Jeps. Univ. Cal. Publ. Bot. **2**:335. 1907.—HOWELL, Fl. N. W. Am. 235. 1900, credits this species to the Northwest, and he is followed by FRYE and RIGG, Elem. Fl. N. W. 159. 1914. JEPSON (*loc. cit.* 335 and 322), however, restricts its range to central California, and we have seen no specimens from Oregon.

4. **Clarkia caurina** (Abrams), n. comb.—*Godetia caurina* Abrams Contrib. Nat. Herb. **11**:410. 1906.—Vancouver Island to western Washington.

5. CLARKIA RHOMBOIDEA Dougl. in Hook. Fl. Bor. Am. **1**:214. 1833.—*Phaeostoma rhomboidea* (Dougl.) A. Nels. BOT. GAZ. **52**:267. 1911.—Eastern Washington and Oregon, and adjacent Idaho to Utah, Nevada, and California.

6. **Clarkia Romanzovii** (Ledeb.), n. comb.—*Oenothera Romanzovii* Ledeb. ex Hornem. Hort. Hofn. Suppl. **1**:133. 1819; *Godetia Romanzovii* (Ledeb.) Spach, Hist. Veg. Phan. **4**:390. 1835.—This species has not been collected since originally by CHAMISSO on "the Northwest Coast," unless a specimen by ELMER from Port Angeles should be referred to it, as suggested by PIPER and BEATTIE (Fl. N. W. Coast 251. 1915). We have not seen this collection; there are, however, two authentic specimens of this species in the Gray Herbarium. One is from the "Hort. Soc. Lond." and the other is from the "Jardin des Plantes, 1837" and belonged to the Gray Herbarium. Both specimens are well preserved and agree with JEPSON'S description (Univ. Cal. Publ. Bot. **2**:349. 1907). PIPER and BEATTIE'S diagnosis is misleading, however, as the plants are not "densely white puberulent throughout" but only so on the young parts, as emphasized by JEPSON, where it is indeed "close and feltlike." Since the species has retained its salient characteristics for generations in cultivation (see JEPSON, *loc. cit.* 321), its rediscovery in a native state is highly probable. Accordingly it seems proper to give it recognition.

7. **Clarkia gracilis** (Piper), n. comb.—*Godetia gracilis* Piper, Piper and Beattie's Fl. N. W. Coast, 251. 1915.—Among our species this is nearest the next, from which it may be distinguished by the united calyx lobes, the tendency of the buds to nod, and the merely puberulent pods. This last character, however, is not dependable anywhere in the genus, as most species show great variation in this respect.

Vancouver Island to Oregon.—OREGON: Silverton, 1871, *Elihu Hall* 192; Tualitin, August 1880, *Joseph* and *Thomas J. Howell* 326; Grizzly Butte, Crook County, June 18, 1894, *Leiberg* 273.—WASHINGTON: Klickitat County, May 27, 1881, *Suksdorf* 23; Bingen, Klickitat County, May 18, 1906, *Suksdorf* 5606.—VANCOUVER ISLAND: Ball Mountain, June 17, 1907, *Rosendahl*, 1849.

8. **Clarkia quadrivulnera** (Dougl.), n. comb.—*Oenothera quadrivulnera* Dougl. in Lindl. Bot. Reg. *pl. 1119.* 1827; *Godetia*

quadrivulnera (Dougl.) Spach, Hist. Veg. Phan. **4**:389. 1855; *G. bingenensis* Sukṣd. Deutsch. Bot. Monatss. **18**:88. 1900.—Vancouver Island to California.

9. **Clarkia viminea** (Dougl.), n. comb.—*Oenothera viminea* Dougl. Bot. Mag. *pl. 2873.* 1828; *Godetia viminea* (Dougl.) Spach, Hist. Veg. Phan. **4**:389. 1835.

Western Oregon to California.—OREGON: Grant's Pass, Josephine County, June 23, 1884, *Howell;* Multnomah County, June, 1877, *Howell* 138 and 139; Coast Ranges, July 1882, *Howell* and *Henderson.*

10. **Clarkia purpurea** (Curtis), n. comb.—*Oenothera purpurea* (Curtis) Bot. Mag. *pl. 352.* 1795; *Godetia purpurea* (Curtis) Don in Smith Hort. Britt., ed. 3, 237. 1839.—HOWELL (Fl. N. W. Am. 234. 1900) includes this species, but the specimens we have seen have come from California, and JEPSON in his revision cites no collections from Oregon. *G. albescens* Lindley, however, was described from plants grown from seeds secured in Oregon by DYER, and since it is probably a form of *C. purpurea*, as suggested by JEPSON (*loc. cit.* 351), it seems advisable to credit the latter species to our flora. The congested inflorescence and generally very shaggy pods are salient characters that ordinarily mark the species at once.

11. **Clarkia Arnottii** (T. and G.), n. comb.—*Oenothera Arnottii* T. and G. Fl. N. Am. **1**:503. 1840; *Godetia Arnottii* (T. and G.) Walpers, Rep. **2**:88. 1843.—This species may usually be recognized easily by the glabrous capsules, but sometimes these are puberulent as in the specimen by SHELDON. Mrs. BRANDEGEE has collected both forms growing together in California. PIPER and BEATTIE (Fl. N. W. Coast 252. 1915) have not indicated this variation.

Oregon to California.—OREGON: Umpqua Valley, June 24, 1887, *Howell* 703; Lower Albina, Portland, July 21, 1902, *Sheldon*, S. 10975.

12. **Clarkia decumbens** (Dougl.), n. comb.—*Godetia decumbens* Dougl. Bot. Mag. *pl. 2889.* 1829; *G. lepida* Lindl., Bot. Reg. *pl. 1849.* 1836, not Howell, Fl. N. W. Am. 234. 1900, which is probably *C. purpurea* or *C. Arnottii.*—JEPSON has shown (*loc. cit.* 350) that the seeds of this plant were first gathered in Oregon. The present status of the species is comparable to that of *C. Romanzovii*,

and according to JEPSON garden specimens display with fidelity the type characters. There is an indigenous specimen, however, in the Gray Herbarium which answers perfectly JEPSON'S characterization (*loc. cit.* 350). It bears no data other than "Wahlamet. Tolmie," and in GRAY'S handwriting the name "*Oenothera decumbens.*" The locality intended is, of course, the Willamette River, which at one time was spelled in several different ways, as, for example, "Wahlamutte" or "Wallamette."

Gentiana Covillei, n. sp.—Aspect of *G. calycosa* and *G. platypetala* to which it is closely related: stems 10–20 cm. high: leaves 6–10 pairs, at nodes gradually approximated upward, the last two pairs involucrating the solitary flower, broadly ovate to ovate-oblong, obtuse to sub-acute: calyx tube half as long as the corolla tube, doubly spathaceous in appearance, being split on opposite sides to the base, one valve bearing two and the other three small teeth, dark purplish-blue but membranous, the conspicuous veins terminating in the minute lance-cuspidate teeth: corolla dark blue, often with red or copper colored spots or blotches, 25–30 mm. long, broadly tubular-campanulate, the sub-oval or reniform lobes less than half as long as the tube, the margins obscurely crenulate-denticulate; the sinus plaits inconspicuous, being very low-triangular, about 1 mm. high: capsule as long as the corolla, stoutly oblong, obtuse, tapering at base to the short stout stipe: seeds 5 mm. long, very numerous, the body narrowly ovate, the excavated hilum sublateral and membranous apical appendage divergent.

In COVILLE'S Report upon the Funston Collection at Yakutat, no. 108, Disenchantment Bay, is referred to *G. platypetala* with some reservation. WALKER'S ample material in excellent condition is probably the same and shows that the calyx, the seeds, and the plaits are very different from *G. platypetala* as described by GRISEBACH. Since we are indebted to COVILLE'S notes and description (Contrib. Nat. Herb. **3**:344. 1896) for the first accurate information concerning the species here named, we wish to dedicate it to him.

The type is *Walker* 935, secured at an altitude of 2000 ft. on grassy slopes above timberline, Mainland, Vixen Inlet, Alaska, August 20, 1915.

NEMOPHILA PEDUNCULATA Dougl., var. **sepulta** (Parish), n. comb.—*N. sepulta* Parish, Erythea **7**:93. 1893; *N. Menziesii* H. and A. var. *minutiflora* Suksd. Deutsch. Bot. Monatss. **8**:133.

1900; *N. sepulta* Parish, var. *minutiflora* (Suksd.) Brand, Pflanzenreich iv. **251**:52. 1913.—BRAND distinguishes this plant from *N. pedunculata* by the fewer-seeded capsules. The latter species normally has 3–6 ovules to each placenta, although frequently only 2–4 seeds are matured. A specific instance in which this occurs is *Baker* 914 from King's Canyon, Nevada, upon which BRAND bases his *N. pedunculata*, var. *Bakeri* Brand (*loc. cit.* 54). Unfortunately, at least some specimens of this collection show only capsules that mature two seeds. This great variation in the number of seeds matured makes it extremely difficult to distinguish the 4-ovuled and 6–12-ovuled forms, since they differ in no other respect and occupy the same range. In fact, they may even grow in close proximity, as illustrated by *Chandler* 6039 and 6037, both from Isabel Creek, Santa Clara County, California, the first representing the typical form and the latter the fewer-ovuled var. *sepulta*. Sometimes the variety has slightly larger flowers that are more or less dotted with dark markings. This form also occurs throughout the range of the typical state and may be known as

NEMOPHILA PEDUNCULATA Dougl., var. **densa** (Howell), n. comb.—*N. densa* Howell, Fl. N. W. Am. **1**:466. 1901; *N. sepulta* Parish, var. *densa* (Howell) Brand, *loc. cit.* 53; *N. nana* Eastw. Bull. Torr. Bot. Club **28**:151. 1901; *N. alata* Eastw., *loc. cit.* 158; *N. reticulata* Suksd. West Amer. Sci. **14**:32. 1903.

NEMOPHILA HETEROPHYLLA F. and M., var. **tenera** (Eastw.), n. comb.—*N. tenera* Eastw. Bull. Torr. Bot. Club **28**:153. 1901; *N. heterophylla* F. and M., subvar. *tenera* (Eastw.) Brand, Pflanzenreich iv. **251**:56. 1913; *N. nemorensis* Eastw., var. *glauca* (Eastw.) Brand, *loc. cit.* 57; *N. fallax* Eastw., *loc. cit.* 156.—CHANDLER (BOT. GAZ. **34**:211. 1902), in his very practical revision of this genus of extremely variable plants, included in one "species" the forms listed, together with *N. nemorensis* Eastw., which BRAND (*loc. cit.* 56) retains as a species distinct from *N. heterophylla*, including in it all specimens of this group which have linear or minute corolla appendages. Specimens with broad, often prominent, appendages in the corolla he refers to *N. heterophylla*. In doing this, however, he fails to show that the degree of development of the scales in the corolla possesses any value for purposes of

practical classification; on the contrary, his reduction of named forms based on the presence or absence or shape or size of the scales in the corolla substantiates CHANDLER'S observations that the variations of these organs do not furnish suitable criteria for the determination of specific values. BRAND attempts to add weight to his maintenance of *N. nemorensis* by the following analysis of its range in relation to that of *N. heterophylla:* "Das Hauptverbreitungszentrum dieser Art scheint die Santa Clara County zu sein, während das der vorigen wohl die Mendocino County ist. In diesen beiden Counties kommt nur eine Art vor, wahrend in den mittleren Counties beide sich finden." This argument, however, loses its force upon the realization that, although these counties are separated by a distance of over 100 miles, they are equally in the coastal region of the state and enjoy essentially identical ecological conditions. Moreover, all the specimens from this region are very similar in foliage and pubescence, but the material secured in the interior portion of the state and in Oregon is almost always more densely pubescent and usually displays a tendency to have bipinnatifid leaves. Accordingly it seems desirable to recognize this inland state form as an ecological variant of the coastal plant, letting one varietal designation include all the forms of the interior regardless of the development of the scales in the corolla. Since BRAND indicated his subvar. *tenera* as being "Die Form des südlichen Oregon und der Sierra Nevada," this name may be retained for these plants.

NEMOPHILA PARVIFLORA Dougl., var. AUSTINAE (Eastw.) Brand, Pflanzenreich iv. **251**:55. 1913.—*N. explicata* Nels. and Macbr. BOT. GAZ. **55**:377. 1913 should be referred here.

PENTSTEMON PERPULCHER A. Nels. BOT. GAZ. **52**:273. 1911.—RYDBERG has expressed the opinion (Bull. Torr. Bot. Club **40**:482. 1913) that *P. perpulcher* and *P. unilateralis* Rydb., *loc. cit.* **33**:150. 1906, are the same. This assertion is strengthened by the statement that he has had the opportunity of comparing cotype material of the former with the type of the latter, "which is deposited in the herbarium of the New York Botanical Garden." This location of the type of *P. unilateralis* is rather puzzling in view of the fact that that species was said originally to be based on "*P. secundiflorus*

A. Gray, Syn. Fl. **2**:263. 1878, not *P. secundiflorus* Benth." Inasmuch as GRAY wrote his description from a specimen or specimens deposited in the Gray Herbarium, one of these collections must logically be taken as the type of *P. unilateralis*, and not a specimen arbitrarily set up as such in another institution. But to return to the question of the relationship of these species. In the first place, the status of *P. unilateralis* seems to depend primarily upon the value of the presence or absence of hair on the sterile stamen as a specific character. Most recent authors, including RYDBERG in his *Flora of Colorado* (306. 1906), have relied upon this character as a means of separating groups of species, and ordinarily it is doubtless of value, especially when accompanied by other characters, including distribution. Now according to RYDBERG'S key (*Fl. Colo.*), *P. secundiflorus* Gray and, in fact, *P. secundiflorus* Benth. (see DC. Prod. **10**:325. 1846), have the sterile stamen bearded at the tip, while in *P. unilateralis* Rydb. it is glabrous. But in *P. perpulcher* A. Nels. the sterile stamen is always bearded, yet RYDBERG would reduce the latter to his species. Obviously the reduction of *P. perpulcher* means the reduction of *P. unilateralis*, and indeed it is very doubtful whether the latter is specifically distinct from true *P. secundiflorus*, as the two forms grow in the same localities in Colorado and seem to possess no constant difference unless the sterile stamen character is reliable. But the case is much stronger for *P. perpulcher*. Both the other species are glabrous, the corollas average a good 2 cm. in length, and the plants range from Wyoming to northern New Mexico. *P. perpulcher* has only been collected in northwestern Idaho, but is frequent throughout that part of the state. Its foliage is decidedly puberulent and the corollas generally run less than 2 cm. in length. The puberulence is suggestive of *P. virgatus* Gray of New Mexico and Arizona, and in spite of the narrow leaves and glabrous sterile stamen of that species *P. perpulcher* is probably more nearly allied to it than to the Colorado species.

In BOT. GAZ. **55**:382. 1913 we proposed var. *pandus* to take care of a plant in which the puberulence extends throughout. We did not notice, however, that the sterile stamen is glabrous. Altogether this plant seems to be related rather to *P. virgatus*, although

it is far removed geographically and has the broad leaves and the aspect of *P. perpulcher*. Since this plant differs in the same manner from its allies as the species previously discussed, it seems advisable to consider it as a species, although further knowledge may show these characters to be of no consequence taxonomically. But in accord with our present interpretation var. *pandus* must become

P. pandus (Nels. and Macbr.), n. comb.—*P. perpulcher* A. Nels. var. *pandus* Nels. and Macbr. Bot Gaz. **55**:382. 1913.

Pentstemon Albrightii, A. Nels., n. sp.—Growing in small dense tufts, or often as single individuals, the crown or crowns furnished with coarse fibrous roots: leaves mostly basal, tufted on the crowns, glabrous, erect, 3–8 cm. long (including the petiole), spatulately oblanceolate, tapering gradually into the petiole, subacute or rounded at apex: stems one or more from each crown, scapose, the leaves if any remote and bractlike, sparsely floriferous for half their length or more, 1–2 dm. high, glabrous except in the inflorescence which becomes glandular pubescent upward: flowers in a more or less unilateral open raceme: calyx small, dark (greenish-purple), the lobes slightly unequal, as long or longer than the campanulate tube: corolla glabrous inside and out, a pale lavender, 9–13 mm. long, the tube slightly or not at all dilated, the limb short and abruptly spreading: sterile filament glabrous, slender, and much shorter than the others: anther cells confluent but not explanate: style as long as the corolla tube, stoutish, with small stigma.

This species is singular in its few-flowered, open, almost simple, secund racemose cyme. A few of its characters suggest the genus *Chionophila*, particularly its rosulate leaves, scapose stems, and greatly reduced sterile filament. The inflorescence is such, however, that the aspect of the plant as a whole is that of *Pentstemon*. The floral, fruit, and seed characters are also those of *Pentstemon*. It lacks those determinative characters of *Chionophila*, namely, the accrescent calyx, the marcescent corolla, and the large strongly angulate seeds.

It was first collected by J. F. Macbride, in 1910, in the Trinity Lake region of Idaho. Then it was secured by Dr. C. C. Albright, of Anaconda, Montana, in 1914, but both of these collections were inadequate and poor. It was tentatively named as given from Albright's material, but until now it has not seemed wise to publish. Fortunately, Macbride and Payson found it again in Idaho and secured an abundance of excellent material. Their no. 3570, from the Josephine Lakes, Custer County, is the type. They also

secured it on Parker Mountain, in the same county, no. 3237. It seems to be alpine, coming in just at timberline, among the straggling, dwarfed, depressed remnants of the forest and persisting for some hundreds of feet higher.

HAPLOPAPPUS EXIMIUS Hall, Univ. Cal. Publ. **6**:170. 1915.—It is refreshing to see technical papers so fully and painstakingly worked out as those by Professor H. M. HALL. He is so evidently fair that his arguments are unusually convincing. Nevertheless, in publishing this species he states so fully the differences that separate the *Haplopappus* segregates as to confirm (rather than otherwise) their validity. Those who take this view will think, therefore, that the name of the above plant should be **Tonestus eximius,** n. n.

Prenanthes hastata (Less.). n. n.—*Sonchus hastatus* Less. Linn. **6**:99, 1831; *Nabalus alatus* Hook. Fl. Bor. Amer. **1**:294. 1834.

CASTILLEJA MINIATA Dougl., var. **Dixonii** (Fernald), n. comb.—*C. Dixonii* Fernald Erythea **7**:122. 1899.—In BOT. GAZ. **61**:45. 1916 we noted the salient characteristics of *C. miniata* and its var. *crispula* (Piper) Nels. and Macbr. Recently our attention has been called to another variation by specimens sent us from Alberni, Vancouver Island, by Professor J. K. HENRY (his no. 9070 in the Gray Herbarium). These differ from typical material of *C. miniata* only in the very thick leaves. This maritime plant has been designated *C. Dixonii* (*loc. cit.*), the type being composed of decumbent or only slightly ascending plants that evidently represent the extreme condition of this variation. *Piper* 4957 from Ilwaco, Washington, is, like the *Henry* specimens, erect or nearly so. The coastal plants, therefore, seem to represent merely an ecological state of typical *C. miniata*, and may be treated varietally.

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NOTES ON OSMOTIC EXPERIMENTS WITH MARINE ALGAE[1]

RODNEY H. TRUE

During the summer of 1899, when the writer was engaged in plant physiological investigations at Woods Hole, he took the opportunity to study the osmotic properties of a number of algae from both fresh and marine waters. These studies were not complete, but since they shed some light on relations which still have much physiological interest, the results are here presented. Moreover, since that time, through the work of MORSE and his associates (**15**), BERKELEY and HARTLEY (**1, 2, 3**), and others, the recalculations of osmotic relationships have resulted in important changes. The bearing of the work of physicists on the problems of physiology has been pointed out by RENNER (**20**), who has done much to resolve the difficulties involved in the question. The osmotic values here dealt with have been calculated according to the newer methods. In some cases the values calculated according to PFEFFER'S (**18**) data are added in order to enable the reader to contrast the values obtained under the two methods of reckoning.

Osmotic pressure in Spirogyra cells

It was desired first to ascertain an approximate measure of the osmotic value of the sea water at Woods Hole. For this purpose some organism having a lower osmotic pressure than that of the sea water was sought. Several fresh water algae, *Spirogyra elongata*(?), *Zygnema* (sp.), and *Oedogonium* (sp.), found growing in a small fresh water pond between Woods Hole and Nobska Point, were tested.

Preliminary experiments with the distilled water available showed the presence of injurious impurities, probably copper from the still. The addition of shredded filter paper to the stock bottle was found to remove the pathological symptoms, and the solutions

[1] Published by permission of the Secretary of Agriculture.

used were made up with distilled water so treated. In all cases solutions were made up on the basis of the desired number of gram molecules of dry substance dissolved in water sufficient to make a liter of *solution*, that is, on the volume-normal basis.

In order to calibrate the indicator plants, solutions of cane sugar and of NaCl in a graduated series of concentrations were carefully prepared from high grade chemicals. These dilutions when in use were kept in covered beakers of 250 cc. capacity. The algae were quickly freed of surplus solution by the use of fresh filter paper before transfer, and freed from remaining traces of the solution by a quick rinsing in a duplicate portion of the solution into which they were to go. After the transfer, filaments were removed at definite intervals for microscopic examination, either on a watch glass or on a slide.

In determining the osmotic equivalent, some difficulty was experienced owing to the fact that all cells of the same filament did not show the same plasmolytic response to a given concentration. This difference was especially marked as the critical concentration was approached. As a rule the tip cells of a filament showed incipient plasmolysis in a weaker solution than did the other cells. Those that had lately undergone division seemed to plasmolyze more promptly as a rule. Since plasmolysis begins to take place only after the concentration of the outer medium is in excess of the concentration of the cell sap, in this study the osmotic end reaction was regarded as reached when the first traces of withdrawal of the protoplast were seen in the tip cells. Since the problem of absorption was not under investigation, the persistence of signs of plasmolysis was not studied. In order to avoid as far as possible complications due to the penetration of the materials from the solution under test, results seen within an hour after the application of the solutions in question were accepted. At times slight plasmolysis seen within this time would soon disappear. Obviously, therefore, the promptest possible registration of osmotic conditions would be expected to give the best evidence of conditions normally existing in the cell.

As a result of a series of tests made with cane sugar, it appeared that for a major part of normal *Spirogyra* and *Oedogonium* cells a concentration of 0.25 gm. molecules per liter of solution was just short of producing plasmolysis at 22°0 C. Only in the tip cells was

an undoubted "starting" of the protoplast from the wall seen. This appeared inside of 20 minutes and still persisted at the end of an hour, but was scarcely noticeable after 20 hours. The osmotic pressure of the cell contents of these algae was, therefore, very nearly equal to 0.25 gm. mol. of cane sugar in a liter of solution. In calculating this value in terms of atmospheres, the values of MORSE and FRAZER (**15**) were used. However, since MORSE'S osmotic determinations were made on the basis of gram molecules dissolved in 1000 gm. of water, this value was reduced to the latter basis by means of RENNER'S formula: $\frac{m \quad 1000}{1000-214m}$, m being the given number of gram molecules in 1000 ccm. of solution. The osmotic equivalent of the algae in question became, therefore, 0.264 gm. mol. in 1000 gm. water. The osmotic values of a series of cane sugar solutions determined in atmospheres by MORSE (**16**) and associates were plotted in a series of curves on which by interpolation the osmotic value of 0.264 gm. mol. weight-normal at 22° C. (the temperature at which the plasmolyzing solutions stood at the time of the determination) was found to be about 6.7 atmospheres. According to PFEFFER the corresponding value would be about 5.9 atmospheres.

Tests on *Spirogyra* showed that the cell contents were osmotically equal to a solution of NaCl containing about 0.16 gm. mol. in a liter of solution. In solutions of NaCl of this degree of dilution the difference between volume-normal and weight-normal is negligible in view of the wide range of error in the biological data. This may be seen by calculating weight-normality in accordance with the following formula given by RENNER (p. 500). When M equals the molecular weight of NaCl (58.5), m equals the number of gm. mol. per liter of solution, and s the specific gravity of the given solution, the corresponding weight-normality equals $\frac{1000m}{1000s-m.M}$. The specific gravity (20°/4° C.) of a 0.16 volume-normal NaCl (0.93 per cent) solution obtained by interpolation on a curve based on LANDOLT-BÖRNSTEIN-ROTH (**13,** p. 260) is about 1.005. Solving the equation, the corresponding value weight-normal is 0.1607 gm. mol. in 1000 gm. water.

The osmotic value of 0.16 gm. mol. NaCl in terms of atmospheres is not so readily deducible in this case as in that of cane sugar, and in view of the physical difficulties discussed by RENNER the writer has taken the corrected osmotic values given by him (p. 501) as a basis of calculation. By interpolation the osmotic pressure of 0.16 gm. mol. NaCl is about 7.2 atmospheres at room temperature. According to PFEFFER this corresponding value would be 5.7 atmospheres.

In this concentration the cell contents became markedly disordered after a short time, the chlorophyll band largely losing its spiral form. However, tests with solutions of cane sugar, slightly stronger osmotically, showed prompt and apparently normal plasmolysis. After 24 hours in this solution the chlorophyll band was still further disordered, although nearly all cells were clearly living and plasmolyzed normally in stronger concentrations.

Osmotic value of sea water

By the use of cane sugar solutions the osmotic pressure of *Spirogyra* here used was found to be about 6.7 atmospheres; the use of NaCl solutions gave about 7.2 atmospheres. Since the difference between these values is without doubt exceeded by the differences in the osmotic pressures prevailing in individual cells of the same filament, there is perhaps little point in discussing which of these values shall be adopted as the basis of further calculations. Hence, an approximate value of 7.0 atmospheres is adopted as the basis of further discussion.

The sea water used was dipped from outside the Fish Commission pier, where it is subject to almost unceasing tidal movement, and gave a density reading of about 1.0210 at 71° F. This was diluted with distilled water in various proportions and used as a plasmolyzing agent for *Spirogyra*. A stage similar to that just noted as indicating beginning plasmolysis was seen in a mixture containing *30 parts* by volume of sea water to *70 parts* of distilled water at 22° C. In this concentration *Spirogyra* and *Oedogonium* agreed in showing faint indications of incipient plasmolysis. *Mesocarpus* showed more distinct traces. These traces disappeared inside of 24 hours.

It appeared from these experiments that the osmotic presure of a 30 per cent sea water solution was approximately equal to about 7.0 atmospheres. By plain calculation the osmotic value of undiluted sea water would be about 23.3 atmospheres.

Since, however, it is well known that salts in aqueous solutions dissociate electrolytically in greater proportion in dilute solution than in greater concentrations, a given number of molecules might through their ionization be expected to cause a proportionally greater osmotic pressure at 30 per cent dilution than in a solution having three times that concentration. In order to get an idea of the general order of magnitude of the change here concerned, it is assumed that the behavior of the sea water approximates that of a half-normal NaCl solution. In this solution, corresponding to the undiluted sea water, about 73 per cent of the molecules would be dissociated at 18° C. (KOHLRAUSCH and HOLBORN, **12**), while a 30 per cent sea water solution corresponding roughly to N/6 concentration of NaCl would be dissociated about 81 per cent. This would increase the relative osmotic value from 173 to 181. This difference amounts to about 5 per cent of the osmotic value of the N/2 solution. To correct for this overestimate would require the subtraction of about 1.0 atmosphere from the first calculation. This would give an osmotic value of about 22.3 atmospheres for the sample of sea water here used.

In this connection it is of interest to compare this approximation with other determinations of this value. The salt content of the sample of sea water used may be calculated from the specific gravity reading 1.0210 at 71° F. This reading, reduced to a basis of specific gravity $\frac{15^\circ C.}{4^\circ C.}$ by means of LIBBEY'S (**14**) table, becomes 1.0216. This value reduced to terms of salt content by the use of PETTERSON'S (**17**) comparison of specific gravity with results obtained by titration of Cl content indicates a total salt content of about 2.93 per cent.[2] Assuming this result to have been approximately correct, it is possible by use of the "Challenger" (**7**) analyses to ascertain

[2] A discussion of the methods of calculating specific gravity and salt content with a diagram for the ready handling of these data is found in Science N.S. **42**:732–735. 1915.

the quantity of principal salts present, and by means of their osmotic equivalents to calculate roughly the osmotic value of the sample of sea water used in this work.

PFEFFER has calculated the osmotic equivalents of solutions of the common salts, giving the atmospheres of pressure exerted by 1 per cent solutions made up on the basis of 1 gm. of salt in 100 ccm. of solution. The recalculation of the osmotic value of NaCl by RENNER already referred to has given a considerably increased value for this salt. There has been no similar recalculation for the other sea salts known to the writer, but since the quantities of salts other than NaCl are small, but a relatively small effect would result from their correction. $MgCl_2$, present in second largest quantity, namely, 0.32 per cent in the sample of water here concerned, was recalculated by the writer in a very approximate way from freezing point values given in LANDOLT-BÖRNSTEIN-ROTH'S (13) tables for the temperature of 22° C., and a value somewhat greater than that given by PFEFFER was obtained. The values here discussed are brought together for convenient reference in table I. A glance at

TABLE I

Salts	"Challenger" proportions	Quantity in sample used	Atmos. press. 1 per cent sol. by vol. Pfeffer	Osmotic values Pfeffer	Osmotic values recalculated
$NaCl$....	0.777×2.93	= 2.28 per cent	×6.09 atmos.	= 13.8 atmos.	17.30 atmos.
$MgCl_2$....	0.109×2.93	= 0.32	×4.98	= 1.6	2.16
$MgSO_4$...	0.048×2.93	= 0.14	×1.93	= 0.3	0.30
$CaSO_4$....	0.036×2.93	= 0.10	×2.00(?)	= 0.2	0.20
K_2SO_4....	0.025×2.93	= 0.07	×2.72	= 0.2	0.20
	0.995	2.90 per cent	equals	16.1 atmos.	20.16 atmos.

this table shows that if PFEFFER'S osmotic values are accepted, the osmotic pressure of sea water falls short of that contained in the experiment described by a ratio of 16.1 to 22.3. On recalculating, the total pressure derived from analytical data exceeds 20 atmospheres.

In this connection it is of interest to compare with these values those obtained by GARREY (10), using the freezing point method. As a result of several freezings, he concluded that for the water of the basin of the United States Fish Commission the average lower-

ing of the freezing point was −1.82° C., corresponding to an estimated osmotic value of about 22 atmospheres at 0° C. (about 23.7 atmospheres at 22° C.). Assuming the osmotic value of a 1 per cent NaCl solution at 22° C. to be 7.6 atmospheres, in accordance with RENNER'S recalculation (p. 501), GARREY'S result would call for a salt content equal to about 3.1 per cent NaCl. According to SUMNER, OSBURN, and COLE (**22**), the water of Buzzard's Bay and Vineyard Sound varies in salt content between 2.84 and 3.29 per cent total salt.

Osmotic pressure of marine algae

An attempt was made to determine the osmotic pressure existing in certain of the commoner bright green forms found abundantly in the neighborhood of Woods Hole.

Cladophora gracilis var. was found growing on rocks below low tide level near the wall in front of the residence building of the United States Fish Commission. This alga grew in a position where the water was constantly changing and where it was not subject to any marked temperature variation.

Enteromorpha intestinalis, according to DAVIS (**6**), is a type belonging characteristically to the region between tide levels, where it occurs attached to stones, shells, and woodwork. At low tide, therefore, it is often subject to a considerable concentration of its cell contents through evaporation.

Chaetomorpha Linum, like *Cladophora*, is not subject to such wide variations, being found characteristically below the low tide mark.

Small tufts of the filaments or pieces of the frond were placed in graduated series of solutions of cane sugar and NaCl and examined with reference to their osmotic behavior.

In the cane sugar solutions *Cladophora* first showed traces of plasmolysis in 0.85 to 0.90 gm. mol. per liter of solution, corresponding to 1.04 and 1.13 gm. mol. in 1000 gm. of water, corresponding to about 28 and 30.7 atmospheres of pressure respectively.

Enteromorpha gave similar results in solutions containing between 0.80 and 0.90 gm. mol. volume-normal, corresponding to about 0.96 and 1.13 gm. mol. weight-normal, representing 25.8 to

30.7 atmospheres, respectively. *Chaetomorpha* required a 0.9 volume-normal concentration (1.13 weight-normal), corresponding to 30.7 atmospheres, to produce the same effect.

In NaCl solutions corresponding results were seen in *Cladophora* in 0.75 to 0.80 gm. mol. volume-normal. RENNER (p. 501) has pointed out that in NaCl the osmotic pressure is proportional to the molar concentration calculated on the liter of solution, 0.1 gm. mol. having an osmotic pressure of 4.5 atmospheres at 18° C. Hence these concentrations correspond approximately to a range between 33.7 and 36 atmospheres. *Chaetomorpha* showed first traces of plasmolysis in 0.70–0.80 gm. mol., corresponding to 31.5–36 atmospheres of pressure.

The reason why an osmotically greater concentration was required in the case of the NaCl solution to give the same result as that seen in the osmotically less concentrated sugar solution is probably to be found in the greater facility with which these algae admit NaCl. It is probable that the surplus atmospheres required in the NaCl solution over the sugar solution roughly mark the greater degree of penetration of the former. The work of JANSE (11) and of DREVS (8) is significant in this connection.

In 1900 and 1901 DUGGAR (9) carried out similar plasmolytic studies on marine algae at Naples and at Woods Hole. The results presented in his paper seem to have been obtained at Naples, since the values are referred to Naples water. Experiments on *Chaetomorpha Linum* made with solutions of osmotic agents in distilled water, as would be expected, showed markedly higher osmotic pressures than the writer found at Woods Hole. At Naples *Chaetomorpha* was found to be isosmotic with 1.26 gm. mol. by volume cane sugar or 1.73 gm. mol. by weight, having an osmotic pressure of about 34.7 atmospheres; with 0.93 gm. mol. of NaCl by volume equal to about 41.8 atmospheres; and with 1.40 gm. mol. by volume of KNO_3. The freezing point of Mediterranean water was found by BOTTAZZI (4) to be $\Delta = -2.29°$ C., corresponding to about 27.6 atmospheres at 0° C., or about 30 atmospheres at 22° C. This is the equivalent of nearly 1 per cent NaCl, or 6.2 atmospheres higher than values obtained at Woods Hole by GARREY. Analyses of Mediterranean water from Naples reported by ROTH (21) gave

a total salt content of about 3.85 per cent, a value which agrees very well with these findings.

In 1901 Reed (19) made a series of plasmolytic determinations with marine algae at Woods Hole and in solutions made up with distilled water found the following osmotic values: *Cladophora* (sp. not given): NaCl isosmotic with 0.7 gm. mol. NaCl by volume, roughly equal to 31.5 atmospheres at 18° C.; cane sugar isosmotic with 0.8 gm. mol. by volume (0.965 gm. mol. by weight), equal to 25 atmospheres of pressure at 18° C. *Chaetomorpha* (sp. not given): NaCl isosmotic with 0.9 gm. mol. by volume, equal to about 40.5 atmospheres at 18° C.; cane sugar isosmotic with 0.9 gm. mol. by volume (1.11 gm. mol. by weight), equal to about 29.5 atmospheres at 18° C.

Osmotic surplus in marine algae

In order to ascertain the turgor pressure of the marine algae, a comparison between the osmotic value of the cells and that of the sea water itself is necessary. To facilitate such a comparison these values are brought together in table II. For such a calculation as

TABLE II

Osmotic pressures of algae at Woods Hole

Algae	Cell contents isosmotic with				
	Cane sugar gm. mol. in liter of solution		Sodium chloride gm. mol. in liter of solution		Sea water per cent by volume
	gm. mol.	atmos.	gm. mol.	atmos.	
Spirogyra elongata	0.25	6.7	0.16	7.2	30 Osmotic pressure of sea water corrected = 22.3 atmos.
Cladophora gracilis	0.85 0.90	28.0 30.7	0.75 0.80	33.7 36.0	
Enteromorpha intestinalis	0.80 0.90	25.8 30.7	.....	.....	
Chaetomorpha Linum	0.9	30.7	0.70 0.80	31.5 36.0	

that here required it is important to adopt a correct osmotic value for sea water. For purposes of this paper 22.3 atmospheres, corresponding to a sea water concentration of 2.93 per cent total salt, is adopted. A glance at the daily density readings made by the United States Fish Commission shows a considerable variation in the salt content of Woods Hole water from time to time, a fact that

should be borne in mind in comparing the results of different observers. It seems from the observations of SUMNER (**22**, p. 53) and his associates that the salt content at Woods Hole is known to vary between 2.84 and 3.29 per cent total salts.

The osmotic surplus found in the algae studied is easily calculated by subtracting 22.6 atmospheres from the observed osmotic pressures. The results of such a calculation appear in table III.

TABLE III

OSMOTIC SURPLUS IN MARINE ALGAE AT WOODS HOLE

ALGAE	OSMOTIC SURPLUS DETERMINED WITH	
	Cane sugar	Sodium chloride
Cladophora gracilis	5.4 atmospheres 8.1	11.1 atmospheres 13.4
Enteromorpha intestinalis	3.2 8.1	....
Chaetomorpha Linum	8.1	8.9 13.4
Average values	6.6 atmospheres	11.7 atmospheres

The strikingly higher values obtained with NaCl are probably due to the penetration of this substance with the consequently higher concentration required to produce traces of plasmolysis. The writer, therefore, is inclined to regard the lower reading obtained with cane sugar as more nearly the true value in this case. It should be borne in mind, however, as COPELAND (**5**) has shown, that this osmotic surplus is subject to influence from external conditions through their effect on nutrition and in other ways.

Summary

1. By means of the plasmolytic method it is shown that the osmotic pressure in the cells of *Spirogyra*, *Zygnema*, and *Oedogonium* found in Nobska Pond, near Woods Hole, Massachusetts, at 22° C., is equal (1) to about 0.25 gm. mol. in a liter of solution of cane sugar, corresponding to 6.7 atmospheres, (2) to about 0.16 gm. mol. NaCl per liter of solution, corresponding to 7.2 atmospheres, and to a 30 per cent sea water solution (sea water = 2.93 per cent total salts).

2. The osmotic value of the sea water sample calculated from plasmolytic experiments was found to be about 22.6 atmospheres. This value determined by the freezing point method by GARREY reduced to 22° C. was 23.8 atmospheres.

3. The osmotic surplus of *Cladophora gracilis*, *Enteromorpha intestinalis*, and *Chaetomorpha Linum* was found to be about 6.6 atmospheres when determined by means of cane sugar, and 11.7 atmospheres for *Cladophora* and *Chaetomorpha* when determined by means of NaCl. The penetration of NaCl is supposed to be largely responsible for the higher value obtained with this salt.

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LITERATURE CITED

1. BERKELEY, Earl of, and HARTLEY, E. G. J., A method of measuring directly high osmotic pressures. Proc. Roy. Soc. London **73**:436. 1904.
2. ———, The determination of osmotic pressures of solutions by the measurement of their vapour pressures. Proc. Roy. Soc. London A **77**:156. 1906.
3. ———, On the osmotic pressures of some concentrated aqueous solutions. Trans. Roy. Soc. London A **206**:481. 1906.
4. BOTTAZZI, F., Archiv. Ital. Biol. **28**:61. 1897.
5. COPELAND, E. B., Über den Einfluss von Licht und Temperatur auf den Turgor. Inaugural Diss. Halle. 1896.
6. DAVIS, B. M., A biological survey of the waters of Woods Hole and vicinity. Sec. 2. Bot. Bull. Bur. Fisheries 31 **1**:451. 1913.
7. DITTMAR, W., Challenger Report. Physics and Chemistry **1**[1]:204. 1884.
8. DREVS, PAUL, Die Regulation des osmotischen Druckes in Meeresalgen. bei Schwankungen des Salsgehaltes im Aussenmedium. Archiv. Ver. Freunde Naturgesch. Mecklenburg **49**:91–135. 1896.
9. DUGGAR, B. M., The relation of certain marine algae to various salt solutions. Trans. Acad. Sci. St. Louis **16**:473–489. 1906.
10. GARREY, W. E., The osmotic pressure of sea-water and of the blood of marine animals. Biol. Bull. **8**:357–270. 1904–5.
11. JANSE, J. M., Plasmolytische Versuche an Algen. Bot. Centralbl. **32**:21–26. 1887.
12. KOHLRAUSCH, F., and HOLBORN, L., Das Leitvermögen der Elektrolyte insbesondere der Losüngen. Leipzig. 1898 (p. 159).
13. LANDOLT-BÖRNSTEIN-ROTH, Physikalisch-Chemische Tabellen. 4 Aufl. Berlin. 1912 (p. 801).

14. LIBBEY, WILLIAM, Report upon a physical investigation of the waters off the southern coast of New England, made during the summer of 1889, by the U.S. Fish Commission Schooner Grampus. Bull. U.S. Fish Commission **9**:397. 1891.
15. MORSE, H. N., and FRAZER, J. C. W., Osmotic pressure and freezing points of solutions of cane sugar. Amer. Chem. Jour. **34**:1–99. 1905; numerous other papers in the same journal in following years.
16. MORSE, H. N., HOLLAND, W. W., ZIES, E. G., MYERS, C. N., CLARK, W. M., and GILL, E. E., The relation of osmotic pressure to temperature. V. The measurements. Amer. Chem. Jour. **45**:554–603. 1911; table copied in Chem. Abstr. **5**:2588. 1911.
17. PETTERSON, OTTO, A review of Swedish hydrographic research in the Baltic and North seas. Scottish Geogr. Mag. **10**:298. 1894.
18. PFEFFER, W., Pflanzenphysiologie 1^2:128, 129. 1897.
19. REED, H. S., See footnote in DUGGAR'S article, p. 476.
20. RENNER, O., Über die Berechnung des osmotischen Druckes. Eine Literaturstudie. Biol. Centralbl. **32**:486–504. 1912.
21. ROTH, J. L. A., Allgemeine und chemische Geologie **1**:524. 1879.
22. SUMNER, FRANCIS B., OSBURN, RAYMOND C., and COLE, LEON J., A biological survey of the waters of Woods Hole and vicinity. Sec. 1. Physical and Zoological. Bull. Bur. Fisheries **31**:1–53. 1913.

INDEPENDENT EVOLUTION OF VESSELS IN GNETALES AND ANGIOSPERMS

W. P. Thompson

(WITH ELEVEN FIGURES)

The possession of vessels by both angiosperms and Gnetales is perhaps the strongest argument, both of those botanists who believe that the angiosperms have been derived from Gnetales, and of those who maintain that the two groups have descended from a common ancestor. It has therefore received much emphasis in all discussions of the origin of angiosperms and of the affinities of the Gnetales. The emphasis which it has received, however, is out of all proportion to the actual study of the vessels themselves.

In a systematic study of the anatomy of the Gnetales (4) which the writer is carrying on, overwhelming evidence has accumulated that, although the completed vessels of the two groups bear a remarkable resemblance to each other, nevertheless their mode of development and their actual origin have been quite distinct in the two groups. In other words, we have in the case of these vessels another of the baffling examples of parallel development.

Evolution of Gnetalean vessel

The typical vessel of *Ephedra*, the most primitive of the Gnetales, is characterized by the occurrence on its end wall of several or many large bordered pits which lack the middle lamella and in which the bordering area is narrow. The end of such a vessel is shown in radial section in fig. 1 and in tangential section in fig. 2. The figures show that this type of vessel differs from the familiar angiospermic type in having several small bordered perforations in place of the single large one of the higher type. Boodle and Worsdell (1), and the writer (4), have shown how this *Ephedra* type of vessel has been evolved from the ordinary tracheid of the coniferous type. The changes involve (1) the enlargement of the whole element, (2) the enlargement of several of the bordered pits

on the oblique end wall, (3) the reduction in the border of these pits, and (4) the disappearance of the tori and middle lamellae. In conservative regions of *Ephedra*[1] all stages in these processes may be found; in other words, there are all gradations between tracheids and vessels. Fig. 3 represents the radial view of the end of a vessel from the young wood of *Ephedra monostachya*. At the very end are typical bordered pits and higher up are seen stages in their transformation into perforations of the ordinary *Ephedra* kind. Such a gradual transformation is not often seen, but various intermediate conditions between bordered pits and perforations are common in conservative regions. Fig. 4 represents a tangential view of a similar end wall and shows clearly the relationship between perforations and bordered pits. For further details of the process the reader is referred to the previous article by the writer (4).

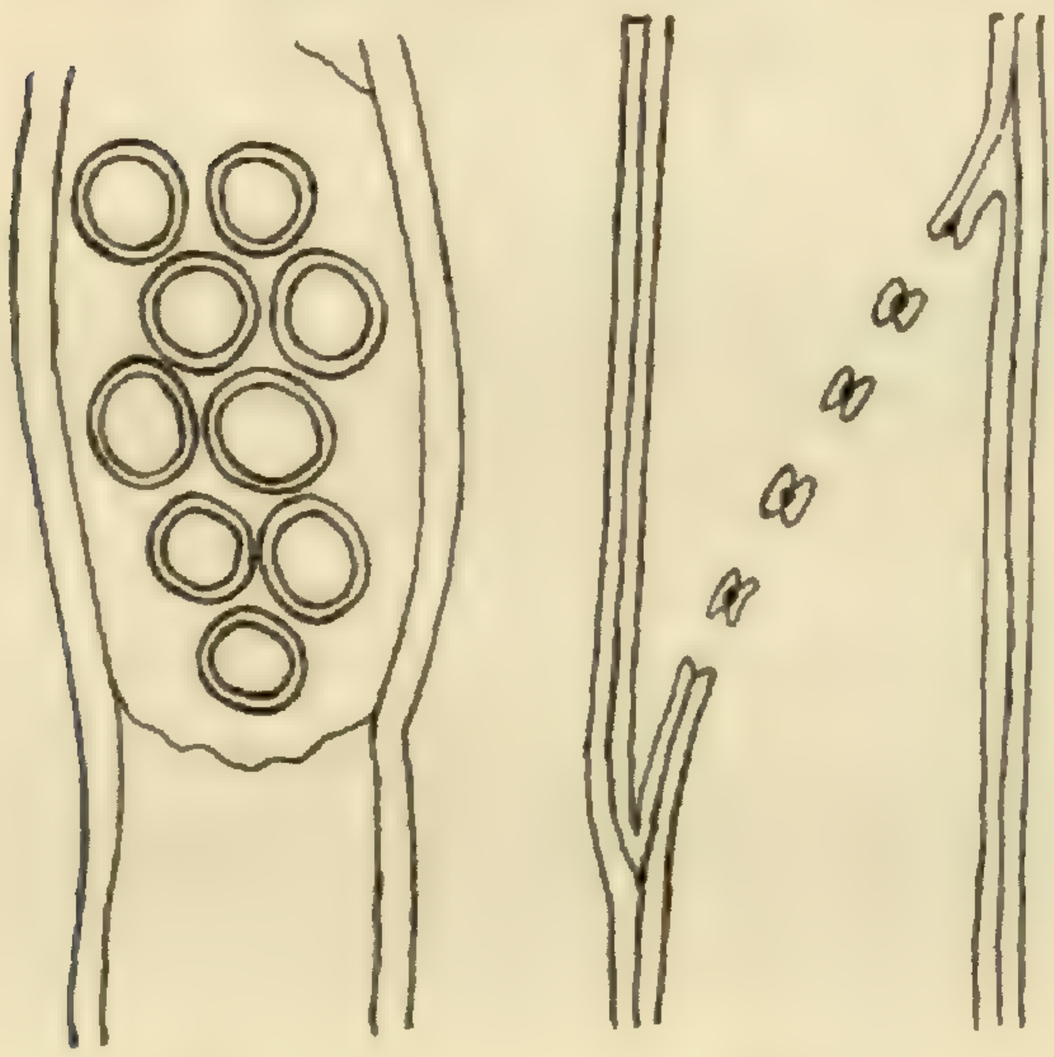

FIG. 1 FIG. 2

FIGS. 1, 2.—Typical vessels from *Ephedra monostachya:* fig. 1, radial; fig. 2, tangential section; all figs. ×250.

The typical vessel of *Gnetum*, the highest of the Gnetales, differs from that of *Ephedra* in having a single large oval or elliptical perforation instead of several circular ones (fig. 5). It is, in other words, like the highest angiospermic type except that as a rule it exhibits a narrow border. Even this

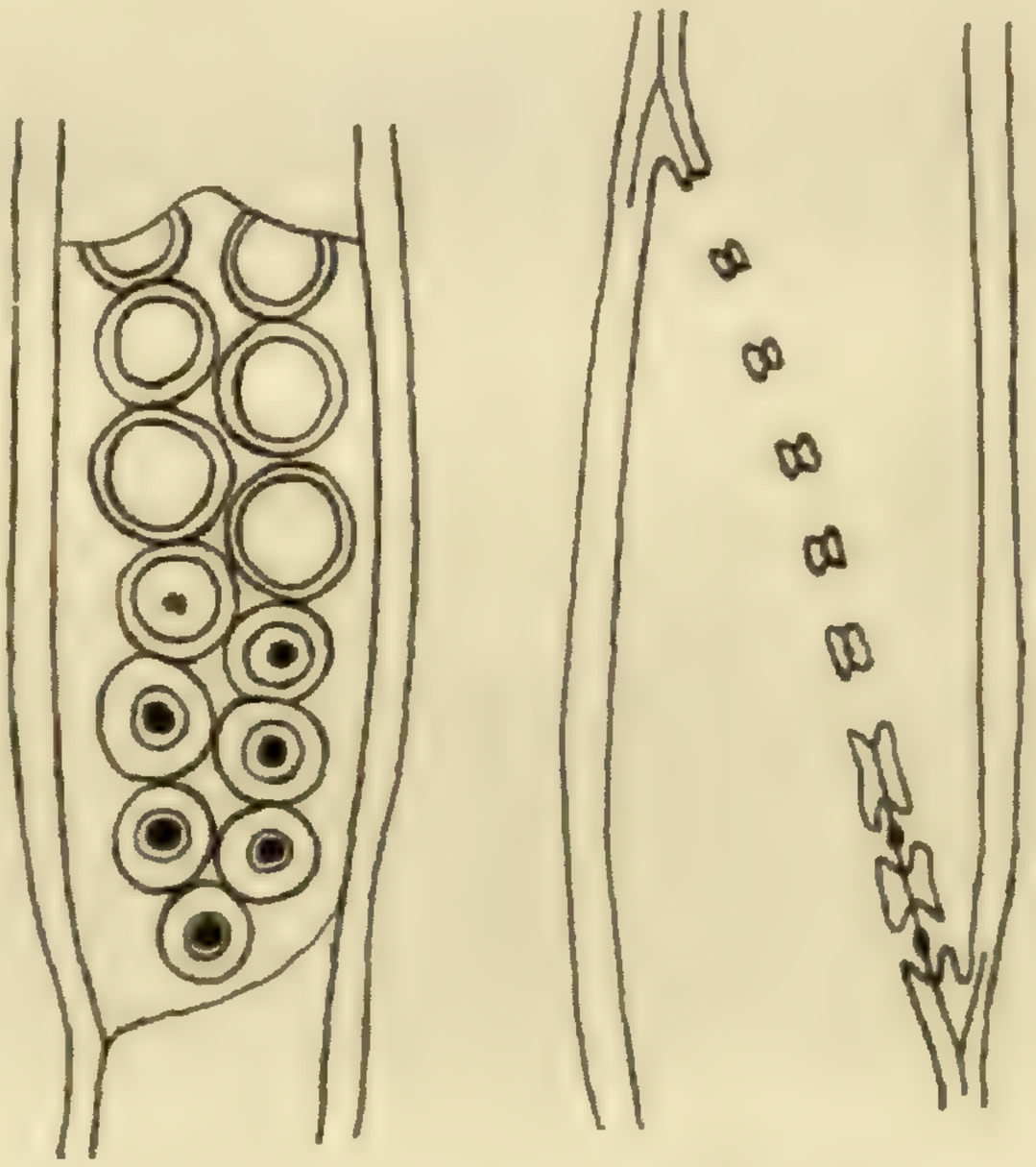

FIG. 3 FIG. 4

FIGS. 3, 4.—Vessels from *Ephedra monostachya*, showing relationship between perforations and bordered pits.

[1] Young stem and root, node, seedling, etc.

border may disappear, however, in the old wood of large trees. In spite of the great differences between the typical vessels of *Gnetum* and those of *Ephedra*, a comparative study of the conservative regions of many species of the former has shown that the *Gnetum* type undoubtedly has been derived from the *Ephedra* type and has revealed the course of its evolution.

FIG. 5.—Typical vessel of *Gnetum*.

In such regions of *Gnetum* the *Ephedra* type of vessel is of common occurrence, as has been noted by DUTHIE (2) and the writer (5). Such a vessel from the young root of a seedling of *G. Gnemon* is shown in fig. 6. Another vessel is shown in tangential view in fig. 7. In this vessel even the relationship to bordered pits is shown. While *Gnetum* naturally does not show the transitions to tracheids as well as *Ephedra*, nevertheless intermediate conditions may easily be found. In some species of *Gnetum* the type of vessel characteristic of *Ephedra* is much more common than in others, and within the same species it is more common in certain conservative regions and certain individual specimens than in others.

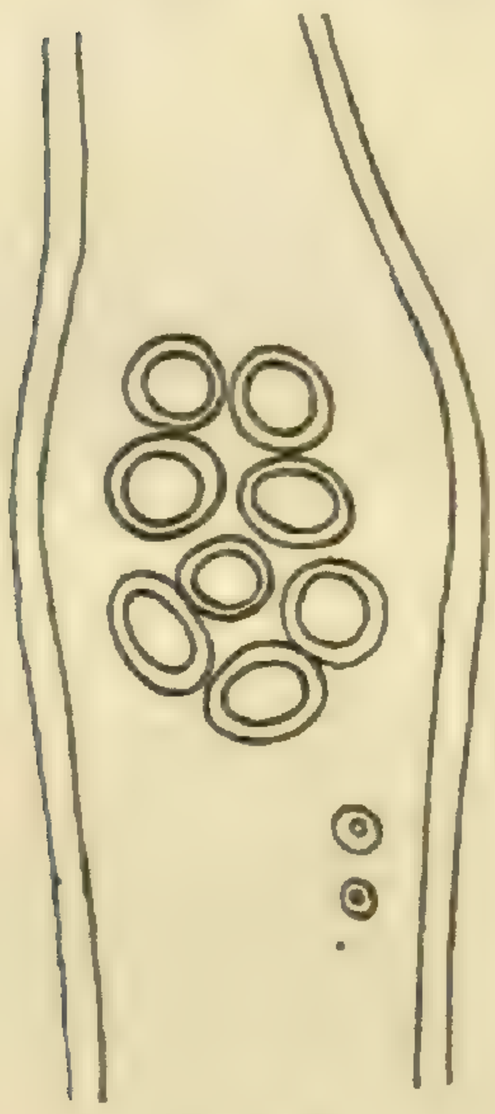

FIG. 6

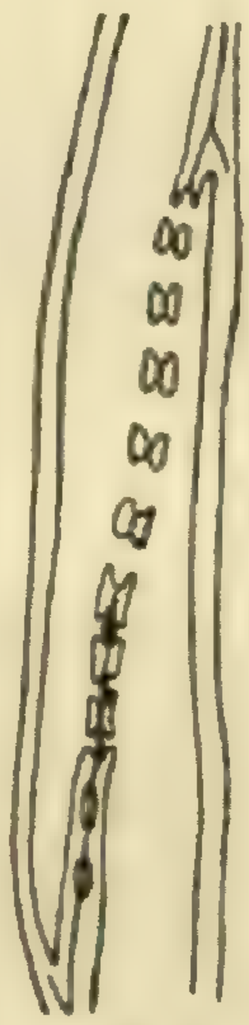

FIG. 7

FIGS. 6, 7.—*Fig.* 6, vessel from root of seedling of *Gnetum Gnemon:* note that it is of the type characteristic of *Ephedra;* fig. 7, tangential section of vessel similar to that shown in fig. 6.

The way in which the *Gnetum* type of vessel has been evolved from the *Ephedra* type is easily observed in such regions and is illustrated in fig. 8. The changes involve the further enlargement of the individual perforations and the disappearance of the portions of the wall between them. In this way the several perforations fuse in a single large one. In fig. 8*a* three of the perforations near the top have fused into a common opening, although parts of their original outlines are still distinct. Near the bottom two pits have fused in similar fashion. At two points (one near the top and the other near the middle) it may be observed that

the pits have fused on the side of one element but not on the side of the other. In fig. 8*c* all have fused in a common perforation on one side but only in groups on the other. In fig. 8*d* the process is nearly completed, the indications of the individual perforations being visible only along the left side. In different vessels all sorts of conditions with respect to the fusion of perforations may be observed. In some cases they first fuse horizontally and in some cases vertically.

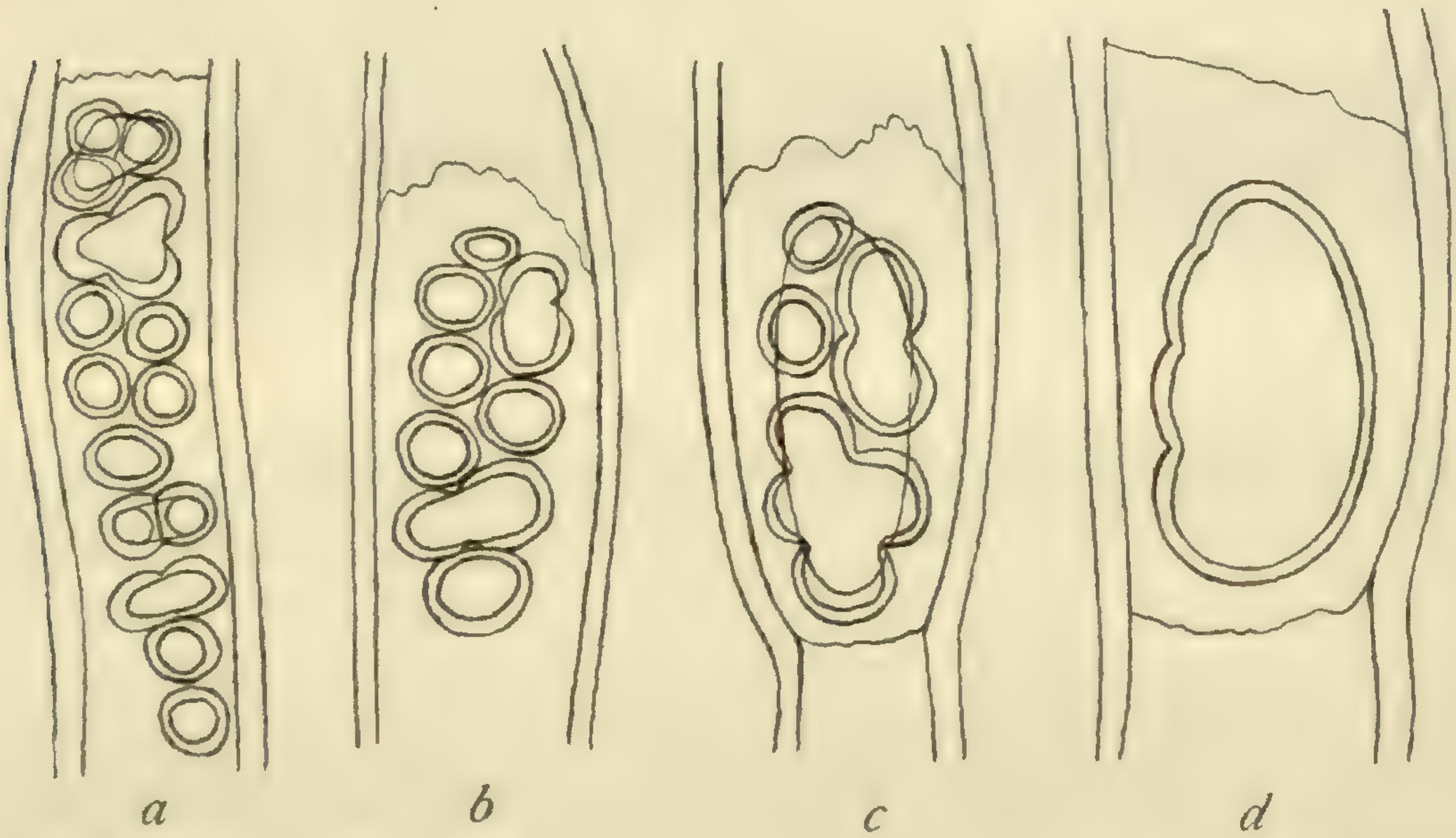

FIG. 8.—Series of vessels from node of seedling of *Gnetum moluccense*, illustrating transitional stages between *Ephedra* type and *Gnetum* type of vessel.

Evolution of the angiospermic vessel

If there is any genetic relationship between the Gnetalean and angiospermic vessels, we should find in the primitive types of the latter a course of development similar to that just outlined, or at least some vestiges of the Gnetalean condition.

The primitive type of angiospermic vessel is undoubtedly the so-called scalariform kind (illustrated in fig. 9 from the wood of *Betula lutea*). The most advanced type is the familiar porous kind with a single large perforation (fig. 10). In the scalariform type the perforation of the end wall is crossed by a large number of parallel horizontal bars, or, in other words, there are many horizontally elongated perforations. The outline of the whole perforated area is similar in shape and size to the single perforation of

the higher type. It is not my intention to discuss the origin of this scalariform vessel in detail. It may be pointed out, however, that such an end wall may have developed in one of two ways.

(1) The scalariform perforations may be modifications of the scalariform bordered pits characteristic of the primary tracheids of all vascular plants and of the secondary tracheids of many ancient forms (*Lepidodendron*, *Calamites*, Bennettitales, etc). If this alternative is the correct one, we have in the angiospermic vessel of this type a retention of a very primitive form of pitting which has disappeared from the secondary tracheids of all plants above the cycads with the possible exception of such plants as *Trochodendron*, *Tetracentron*, etc. (**6**). With the exception of these perforations it is also absent from the vessels of all angiosperms, although JEFFREY and COLE (**3**) regard as vestiges of vessels certain elements with this kind of pitting which they have found in wounded *Drimys* and which occur normally in *Trochodendron* and *Tetracentron*. According to one alternative, therefore, the angiospermic vessel has been produced when the scalariform bordered pits on the end wall of a tracheid lost their membranes and became perforations. At the same time the pits of the lateral walls were transformed into the familiar crowded circular type.

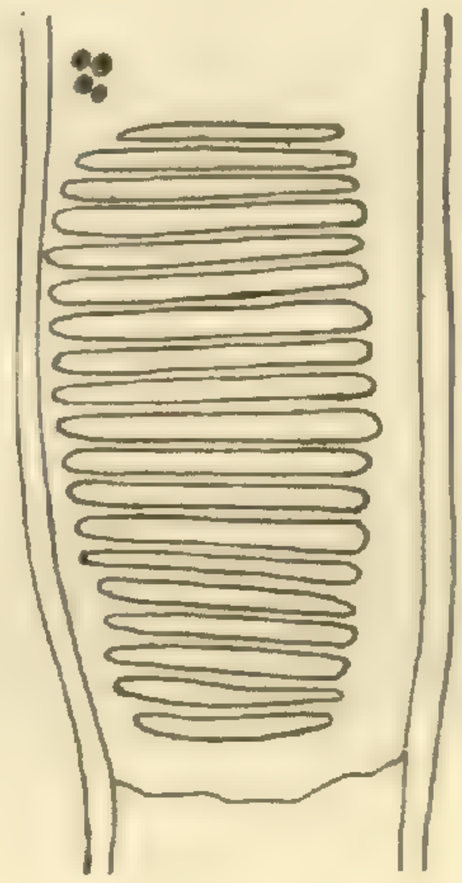

FIG. 9.—Scalariform vessel of birch.

(2) On the other hand, the scalariform perforations may have resulted from the fusion of pits of the ordinary circular multiseriate type. In many angiospermic woods all gradations may be observed between scalariform and multiseriate circular pitting. If this alternative is correct, the angiospermic vessel has not been derived from the primitive tracheid with scalariform pits, but from the higher ordinary type of tracheids with circular bordered pits. The perforations are therefore not retentions but new productions. It

FIG. 10.—Typical angiospermic vessel from *Vaccinium corymbosum*.

should be pointed out that on the basis of the first alternative the transitions between multiseriate and scalariform pitting are to be interpreted in the reverse direction, the multiseriate pits having been derived from the scalariform.

But, no matter which of these two views is the correct one, it is plain that the vessel with the scalariform end wall is the primitive kind in angiosperms. One evidence that this is true is the fact that it prevails in those angiosperms which are admittedly primitive, whereas the type with the single large perforation prevails in the higher forms. Sometimes the two types are found in different members of the same family, but in such cases the more primitive members of the family are characterized by the possession of the scalariform type, while the higher members have the singly perforated type.

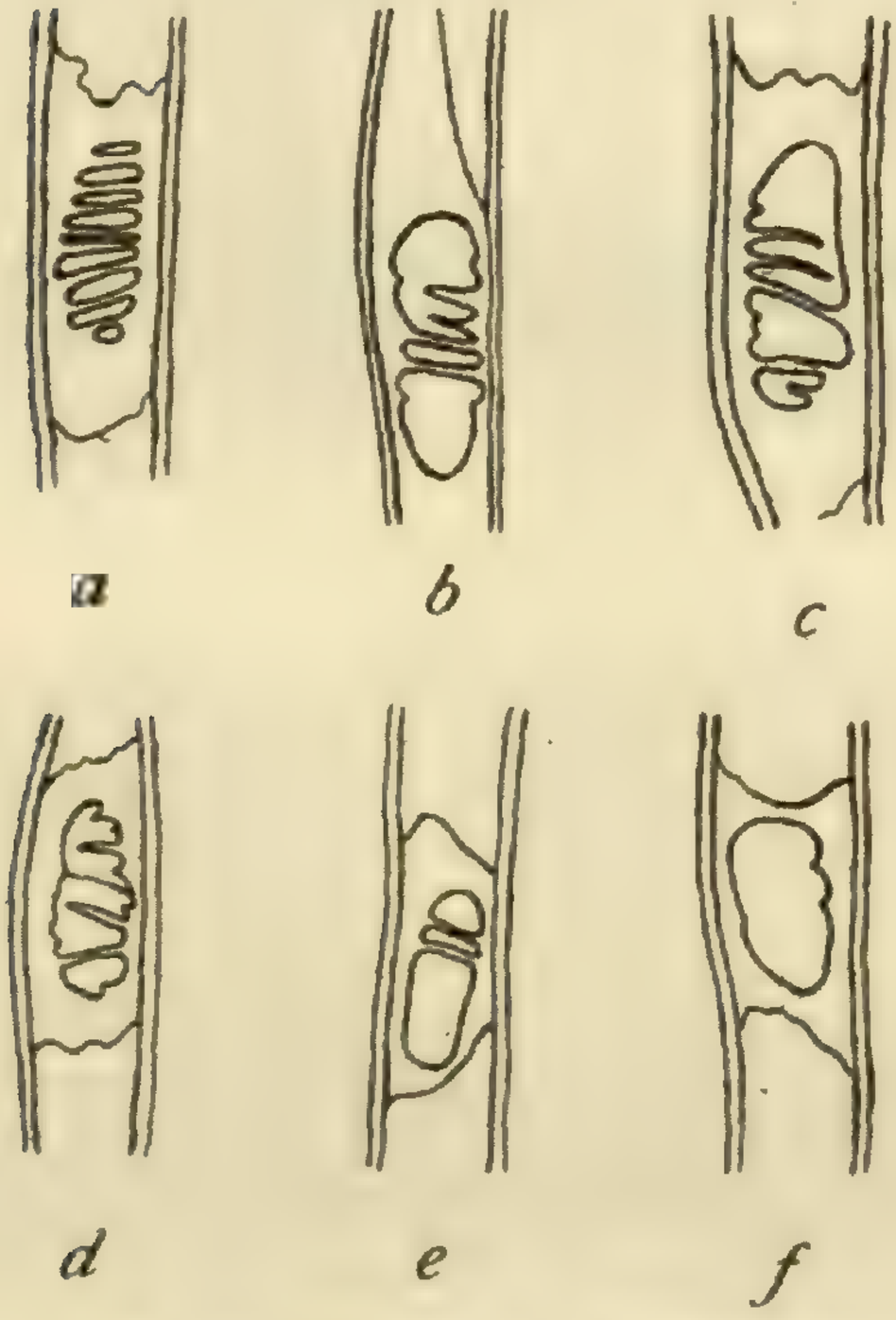

FIG. 11.—Series of vessels from wood of *Vaccinium corymbosum*, illustrating transformation of scalariform perforations into single large perforation.

That the scalariform type of vessel is the primitive one is further shown by cases of actual transformation of this kind into the kind with the single perforation. Not only do these cases prove the primitiveness of the former, but they also give us a picture of the evolution of the single perforation.

Some years ago the writer discovered in the wood of *Vaccinium* all transitions between the scalariform perforations and the single large perforation. The process consists simply of the gradual loss of the bars. Some stages are represented in fig. 11. A typical scalariform vessel is shown in *a;* in *b* two bars remain intact, two more are incomplete, and the positions of others are indicated by the projections from the sides. Random samples further illustrating the process are represented in *c* and *d*. In *f* the process is nearly

completed, the positions of three bars being indicated by projections. In the wood of different species of *Vaccinium* innumerable conditions similar to these may be found side by side. I have been careful to determine that none of these cases are due to imperfect sectioning, but that they represent the actual state of affairs. This has been done by means of careful series of sections in celloidin. Moreover, views like *e*, which are common, could not be produced by the carrying away of the bars in sectioning, for in that case the margin of the perforation would not be smooth, but would show where the bars had been broken. From these facts it is clear that the angiospermic vessel with the single large perforation has been derived from that with the scalariform perforations.

Comparison of evolution of Gnetalean with that of angiospermic vessels

We have seen that the single large perforation of the Gnetalean vessel has been produced by the fusion of several perforations derived from circular bordered pits. We have also seen that the similar single large perforation of the angiospermic vessel has been evolved from the scalariform type. Evidently, therefore, the two are not genetically related. In the evolution of the Gnetalean vessel there is and can be no scalariform stage. The Gnetalean vessel usually has only two rows of circular pits and never more than three. Consequently, no matter how the fusions take place, no scalariform bars can result. The Gnetalean and angiospermic vessels may or may not have been derived from the same type of element, but from the very beginning the evolution of the two has taken place along entirely different lines. In the Gnetalean line a few circular bordered pits, haphazardly arranged, have enlarged and fused in a single perforation; in the angiospermic line long narrow parallel slits, which have been retained or evolved, have fused to form a similar single perforation.

Conclusions

From these considerations it follows that the vessel of *Gnetum* should disappear from all discussions of the origin of angiosperms. The possession of vessels by the two groups can no longer be used

as a demonstration or even as evidence of genetic connection between them; it is rather to be used as a remarkable illustration of development by different plants of the same highly specialized structure. It is to be compared with the independent evolution in lycopods, horsetails, and ferns of similar seedlike structures. To what extent this applies to other points of resemblance between Gnetales and angiosperms is reserved for future discussion.

Summary

1. The vessel of *Gnetum* with the single large perforation in its end wall has been evolved by the enlargement and fusion of several haphazardly arranged bordered pits.

2. The vessel of angiosperms with the similar single large perforation has been evolved from the type with many long, narrow, scalariform perforations.

3. On account of the entirely different courses of evolution by which they were produced, there can be no genetic connection between the vessels of the two groups. They furnish a remarkable illustration of independent development of similar structures.

4. The possession of vessels by both angiosperms and Gnetales cannot be used as an argument in favor of the derivation of angiosperms from Gnetales or of both from common ancestors.

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LITERATURE CITED

1. BOODLE L. A., and WORSDELL, W. C., Some points in the anatomy of Casuarinaceae and Gnetaceae. Ann. Botany **8**:231–264. 1894.
2. DUTHIE, A. V., The anatomy of *Gnetum africanum*. Ann. Botany **27**:593–602. 1912.
3. JEFFREY, E. C., and COLE, R. D., Experimental investigations on the genus *Drimys*. Ann. Botany **30**:359–369. 1916.
4. THOMPSON, W. P., Anatomy and relationships of Gnetales I. *Ephedra*. Ann. Botany **27**:1077–1104. 1912.
5. ———, Morphology and affinities of *Gnetum*. Amer. Jour. Bot. **3**:135–184. 1916.
6. THOMPSON, W. P., and BAILEY, I. W., Are *Tetracentron*, *Trochodendron*, and *Drimys* specialized or primitive types? Mem. N.Y. Bot. Gard. **6**: 1916.

A COLUMELLA IN MARCHANTIA POLYMORPHA

J. E. CRIBBS

(WITH PLATES I, II)

Introduction

Marchantia polymorpha, because of its wide distribution and common occurrence, has long been used as a representative of the Marchantiaceae for laboratory study. The large number of sporophytes appearing upon a single receptacle gives excellent opportunity to obtain various stages of development without much difficulty. Notwithstanding the wide usage of this species and the abundant literature dealing with the development and anatomy of the Marchantiaceae, it appears that in the organization of the capsule the tendency to develop a columella has never been recorded.

In the work of LEITGEB,[1] KIENITZ-GERLOFF,[2] and others observations are given on the development of the elaters within the capsule; and in each case these have been found to be irregularly disposed, appearing as elongated cells which are at first quite indistinguishable from the sporogenous cells, but soon may be detected by their failure to develop transverse walls. The present paper is concerned with some unusual incidents which may occur in the organization and development of these sterile tissues.

The material from which these observations were made was collected during the first week of September 1914. It was taken from an exposed area which had been cleared during the previous fall and burned over. As is frequently the case in such instances, it developed here in dense formation during the following summer. My attention was first attracted to the appearance of columnar structures during the spring of 1915 while preparing material from this collection. Further study of a large quantity from this locality gave one additional instance of this type of organization.

[1] LEITGEB, HUBERT, Untersuchungen über die Lebermoose. Vol. 6. 1881.

[2] KIENITZ-GERLOFF, F., Vergleichende Untersuchungen über die Entwickelungsgeschichte des Lebermoossporogons. Bot. Zeit. **32**:161. 1874; **33**:777–782. 1875.

Because of the dryness of the season and the infringement of more advanced stages of vegetation it was impossible to secure additional material from this locality during the fall of 1916.

Investigation

Two stages were observed in the organization of a central column of sterile tissue within the capsule. Fig. 1 gives a conception of the extent of development in the simpler of these. It may be seen that the close assemblage of a large number of elaters in the center has resulted in almost complete sterilization there. It will be observed in this case, too, that the central column was not originally composed entirely of cells which developed elaters, but mixed with these were sporogenous cells which disorganized before they could form tetrads, leaving protoplasmic remains which take stains deeply. It is doubtful whether the disintegration of these is to be interpreted as a source of additional nutriment for those which remain, or is in any way to be associated with this behavior which is characteristic of members of the Jungermanniales. It seems rather to be an occurrence associated with the unusual, close development of sterile tissue, for it may be observed that immediately outside of this zone there is no such behavior. The capsule, in this instance, has developed to the point where the spores have become isolated from the tetrads, and the elaters are beginning to develop the spiral thickenings characteristic of their walls. These are laid down beneath the more or less spirally disposed protoplasm which is conspicuous at this stage. This columnar development is not the result of assembling the normal number of elaters into a central position, for the diffuse arrangement so characteristic of the species is still maintained in the rest of the capsule; nor is the number, excluding those in the central column, in any way reduced from the normal average.

In the second stage of development (figs. 2, 3) there has been a complete elimination of sporogenous cells, so that the columella is composed of sterile tissue only. The sporophyte in this case was less mature than that represented in fig. 1. The scattered elaters show an almost evenly distributed protoplasmic content which has not yet collected preliminary to the formation of the spiral thicken-

ing. The sporogenous cells are in the compact spore stage following the development of tetrads.

The columella, which at this stage is clearly defined, extends from the base of the capsule through more than three-fourths of its length. It is composed largely of elaters which diverge slightly at the free end. Intermingled with the elaters occur tissues developed from sporogenous cells which have elongated and divided transversely a number of times, but failed to reach the spore mother cell stage; thus remaining as elongated sterile chains of cells which will not develop into elaters, but may, as in fig. 1, completely disintegrate during the later history of the capsule, or in this more compact columella there may be but a partial disorganization. This type of structure, judging from its position and development, is suggestive of the elaterophore of *Pellia*. It has a less advanced state of organization, however, since there is no apparent tendency either to diminish the number of diffusely scattered elaters or to assemble them at the apex of the column.

Another phase in the development of sterile tissue within the capsule is met with in the group of cells which occur at the apex. The development of sterile cells at this point at once recalls the condition existing in *Aneura*. KIENITZ-GERLOFF refers to the development of two layers of sterile cells here. Examination of a large number of sporophytes, however, will show that there is considerable variation in the amount of this tissue, and also that it may be formed in different ways.

Fig. 4 represents a young sporophyte when the greater density of the protoplasm in the distal half is just becoming manifest. There has been no separation of sterile tissue at the apex up to this stage. In this instance two eggs have been developed in the venter, only one of which is seen to be developing an embryo. It would seem, from the fact that all the other eggs developed on this receptacle were fertilized and forming sporophytes, that the failure of this one to do so may be attributed to a potential sterilization which follows the initial development of the egg first fertilized, a response comparable perhaps to that of *Pellia* or *Pallavicinia*, where but one sporophyte regularly develops from a group of closely assembled archegonia.

When the sporophyte has attained the stage immediately preceding the invasion of the gametophytic tissue by the developing foot, the first isolation of cells which will contribute definitely to the apical group may sometimes be observed (fig. 5). The first isolation is suggested by the appearance of more pronounced cell walls. In the structure of the cells themselves at this stage there is usually no observable difference; but when once the foot establishes itself, and the sporogenous cells rapidly increase in density and begin elongation, these become more prominent because of their less density, their more conspicuous nuclei, and their failure to undergo elongation.

In most cases a single layer of cells is formed, cut off at this early stage, although occasionally two layers in addition to the wall cells will be found. These originally isolated cells are commonly carried forward at the apex as the sporogenous cells below them continue their elongation; and they generally compose all there is of sterile tissue here, but not uncommonly the amount is increased in one of two ways. The sporogenous initials may by periclinal divisions contribute to the mass just before the rapid series of anticlinal divisions which accompanies the broadening of the capsule and elongation of the sporogenous cells (fig. 7). Moreover, the bulk of sterile tissue may be increased by the division of wall cells near the apex (fig. 6). The contribution by this method is apparently very slight and less common than by the former. A third method by which the tissue may be increased in bulk would be by continued division of the sterile cells after their first isolation. Although this would seem a very probable occurrence, I was unable to observe any direct evidence of it. The apical end of a more mature sporophyte is shown in fig. 8. The sporogenous cells are in the tetrad condition, and the close association of the elaters with the sterile cap toward which they converge is very conspicuous.

Conclusions

In the Marchantiaceae, the first family of the Bryophytes in which there occurs any sterilization of potentially sporogenous tissues, the elaters are commonly diffusely arranged; but in

Marchantia they sometimes develop so abundantly in the center of the capsule as to produce a columella.

Intermingled with the elaters occurs considerable tissue derived from sporogenous cells which undergo elongation and divide frequently, giving rise to chains of cells. These fail to reach the spore mother cell stage, and may persist for a considerable time. They either partially or completely disorganize, however, about the time the elaters develop their wall thickenings.

The disintegration of these sporogenous cells is a feature limited to the columella, and apparently is not essentially a nutritive function, but is a condition arising from the close grouping of the central elaters.

A columella of this type strongly suggests the elaterophore of *Pellia*, and is an advancement in the organization of the sterile tissues of this family along the same line of development that regularly appears in members of the Anacrogynae.

That this unusual occurrence may be attributable directly to external factors is highly improbable; but should be considered the first stage in the tendency to break up the sporogenous mass, a feature very prominently displayed in the sporophyte as it increases in size and complexity.

The initial separation of sterile cells at the apex may occur even before the intrusion of the proximal part to form the foot, or it may first be recognized at the time of the initial elongation of the sporogenous cells.

The group of cells thus separated at the tip may be added to either by the division of the wall cells, or by periclinal walls in the elongating sporogenous cells.

This occurrence of a cap of sterile cells at the apex of the capsule is likewise a feature appearing prominently in members of the Anacrogynae, where in *Aneura* it bears attached elaters. The occasional appearance of three or four layers of sterile cells at the tip, and the convergence of the elaters, together with the close relation they frequently bear to this point, are further evidences of transitional features from the diffuse arrangement of elaters to a definite organized structure such as the elaterophore found in members of the Jungermanniales.

I wish to express my appreciation of the helpful criticism of Dr. W. J. G. LAND.

UNIVERSITY OF CHICAGO

EXPLANATION OF PLATES

Fig. 3, ×63; all others, ×450

FIG. 1.—Simple columella at time of separation of spores from tetrads, showing dense cluster of elaters and disorganized sporogenous tissue.

FIG. 2.—Columella immediately preceding thickening of elaters; composed largely of chains of sporogenous cells which failed to reach spore mother cell stage.

FIG. 3.—Median view of sporophyte giving topography.

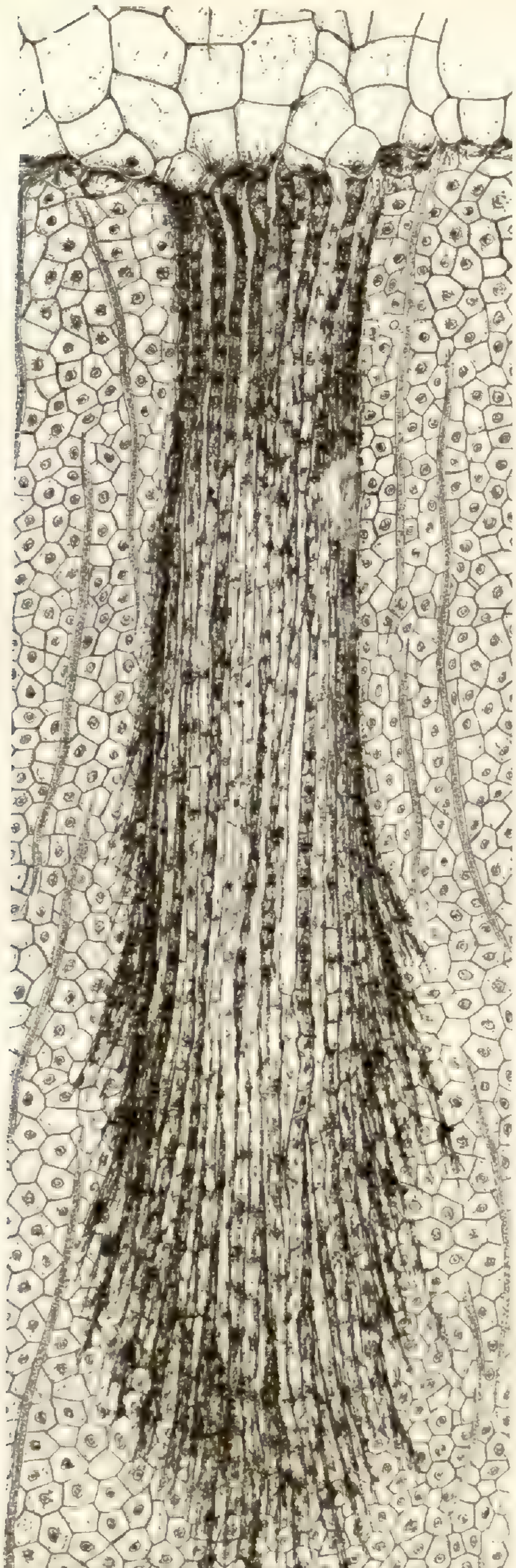
FIG. 4.—Young sporophyte preceding isolation of sterile cap cells; unfertilized egg beside sporophyte.

FIG. 5.—First isolation of sterile cap cells preceding elongation of sporogenous cells.

FIG. 6.—Cap cells readily distinguished at time of invasion of foot; wall cells contributing to sterile cap group.

FIG. 7.—Unusually large mass of sterile cells, 4 deep at apex.

FIG. 8.—Close relation of radiating elaters to apical group, tetrad stage.



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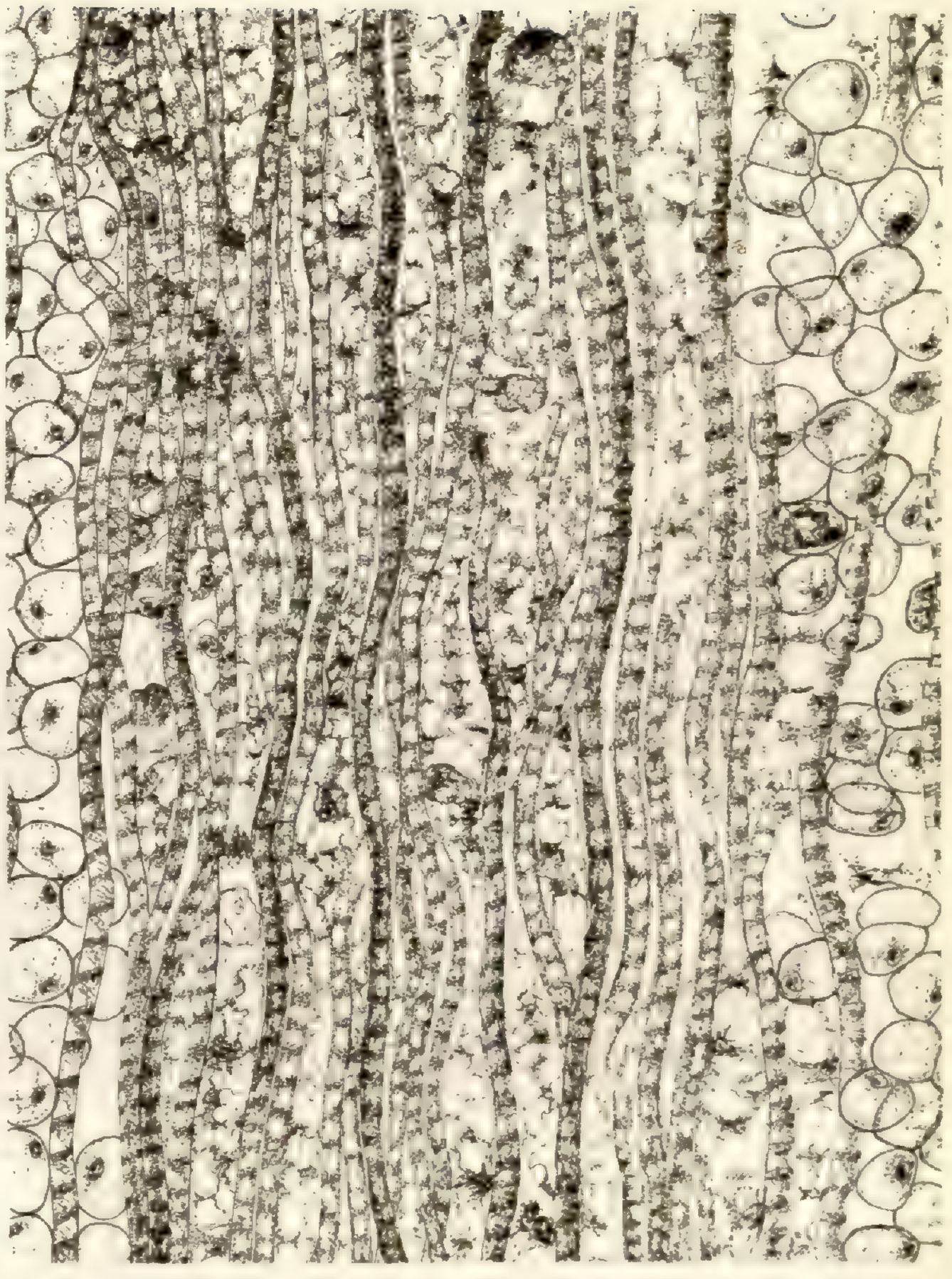

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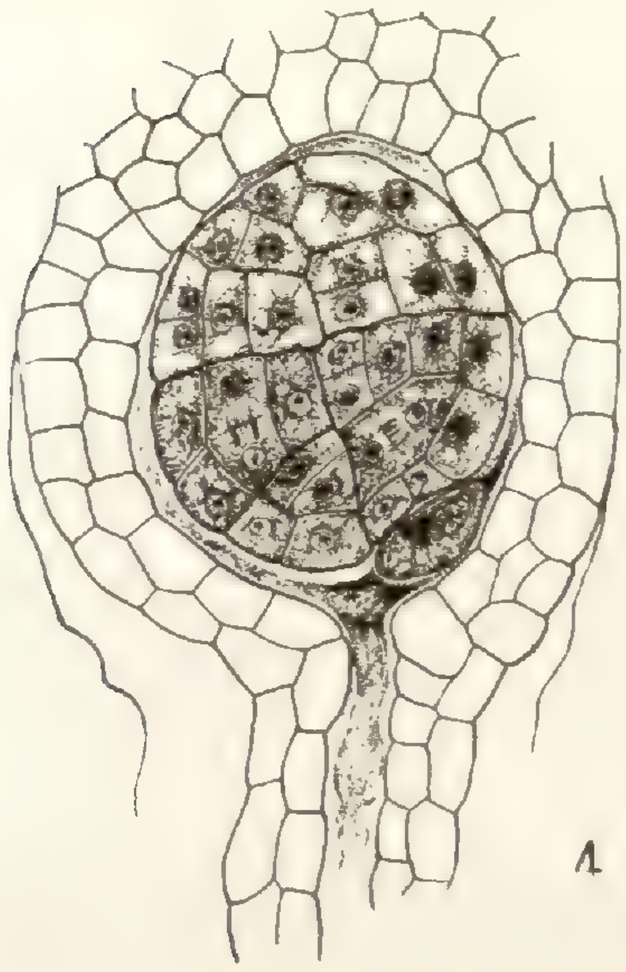

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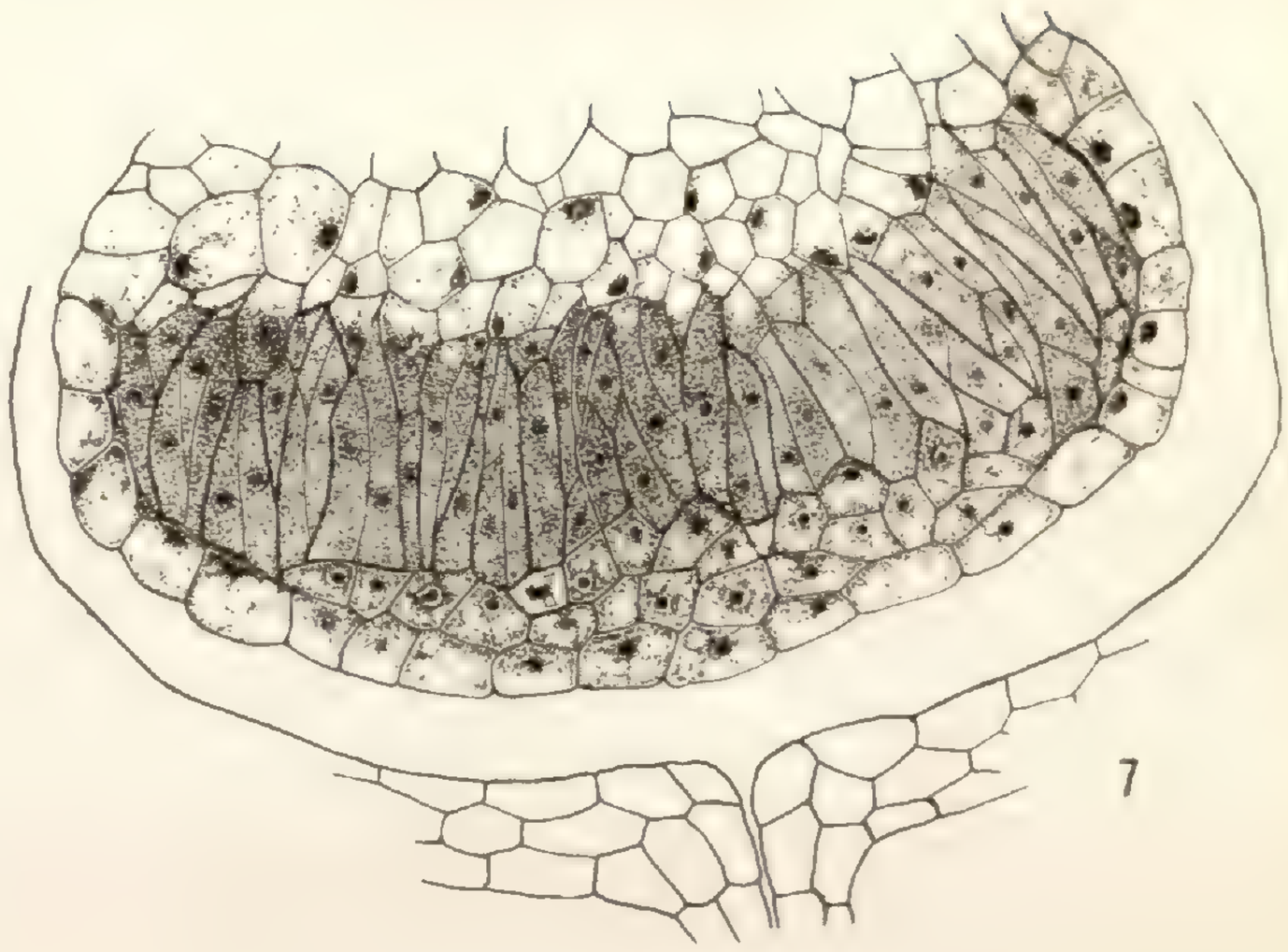

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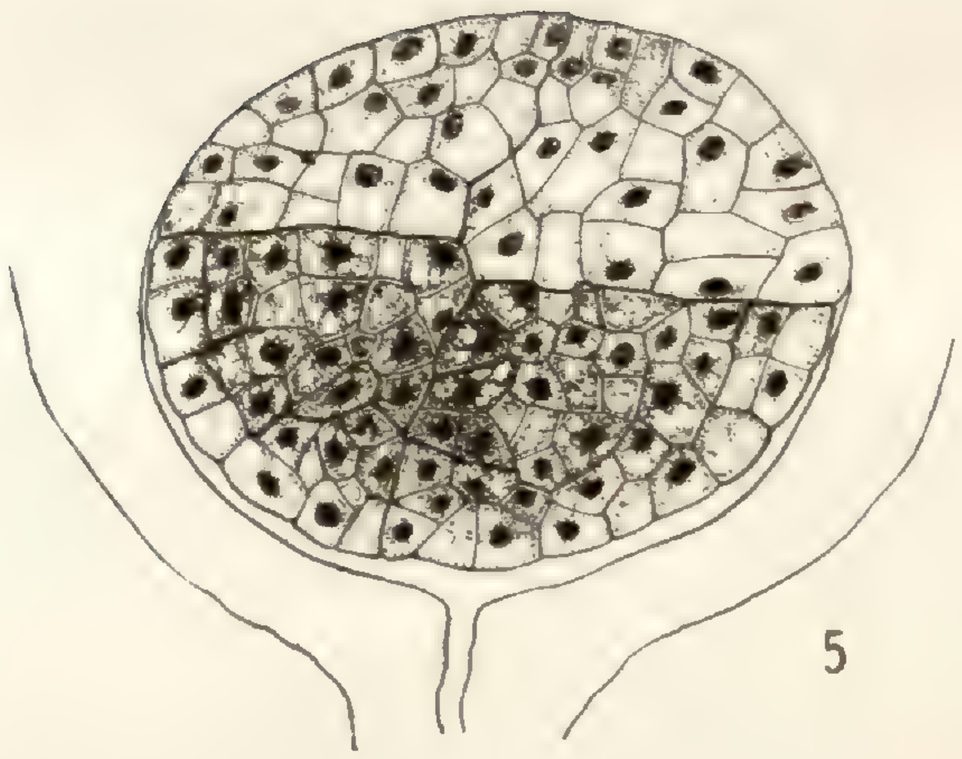

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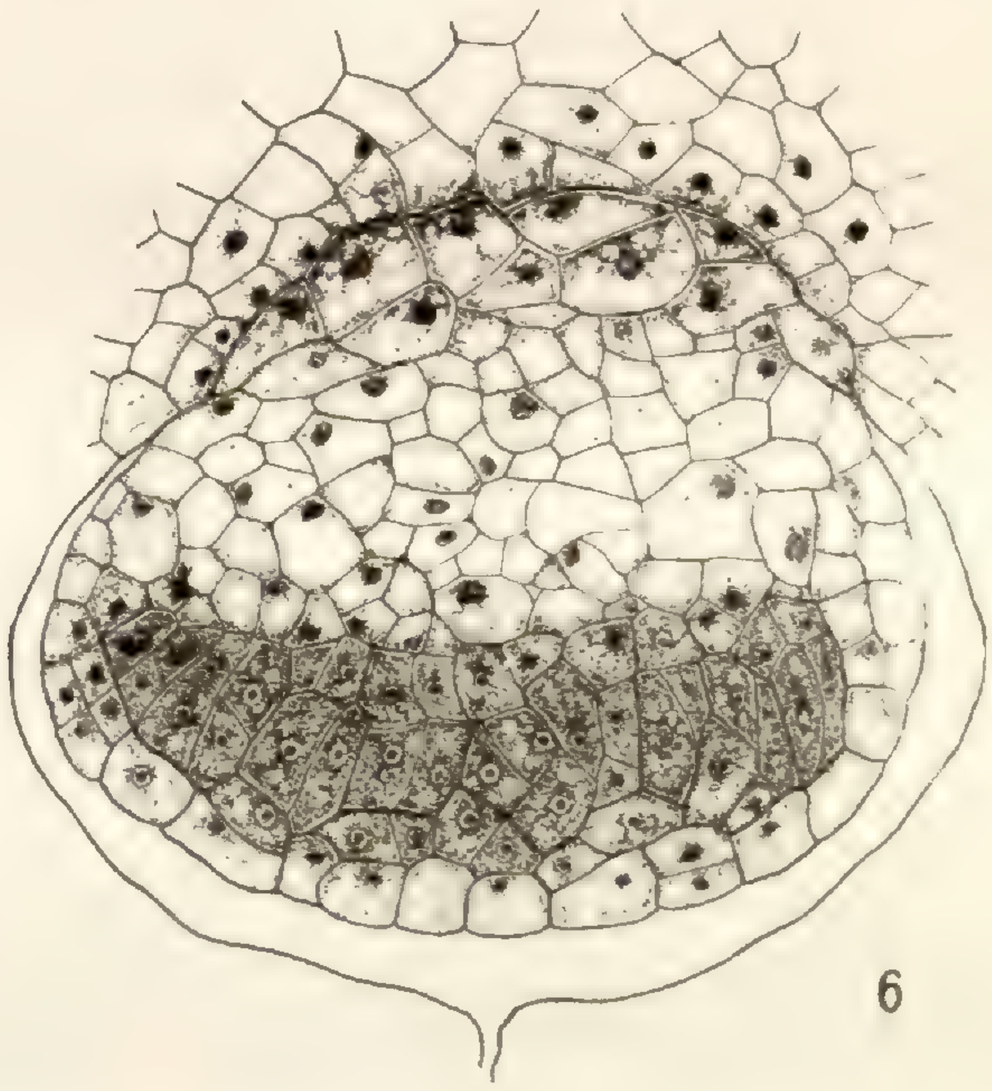

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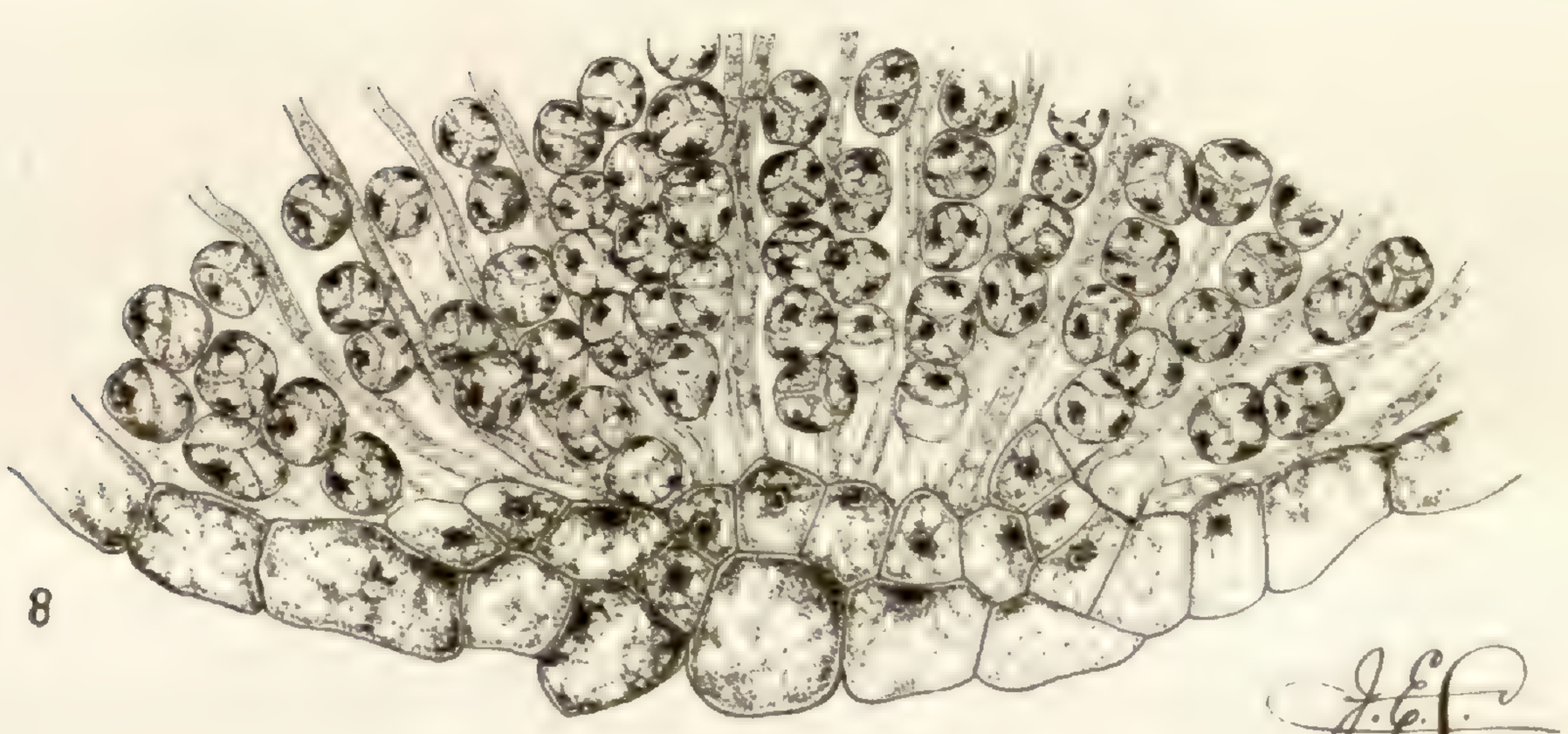


8

CRIBBS on MARCHANTIA

APOGAMY IN THE CYATHEACEAE

ALMA G. STOKEY

(WITH TEN FIGURES)

Since the discovery of apogamy in *Pteris cretica* by FARLOW (3) in 1874, it has been observed in about 15 genera and 30 species of the Polypodiaceae. There are records of its occurrence in 3 other families of the Filicales, namely, the Osmundaceae, the Hymenophyllaceae, and the Marsiliaceae. It has been reported by SADEBECK (9) in *Todea africana*, by LEITGEB (7) in *Osmunda regalis*, by STANGE (12) in *Todea rivularis* and *T. pellucida*, by BOWER (1) in *Trichomanes alatum*, by WORONIN (14) in *Trichomanes Krausii*, and by SHAW (11) and STRASBURGER (13) in *Marsilia*.

For several years I have been making a study of the prothallia of the Cyatheaceae, most of the results of which will appear in a later paper. I have had under cultivation 13 species belonging to 5 of the 7 genera. The species studied include 6 species of *Alsophila*, 1 of *Hemitelia*, 2 of *Cyathea*, 2 of *Dicksonia*, and 2 of *Cibotium*. I am indebted to Dr. J. M. GREENMAN for the determination of all the species with the exception of *Alsophila Cooperi* F. Muell., which was obtained from the greenhouses of Harvard University, and *Cyathea muricata* Wild. (*Alsophila muricata* Desv.), obtained from the New York Botanical Garden.

In order to obtain pure cultures it was found necessary to take measures to remove foreign spores from material obtained from greenhouses where other ferns were growing. The leaves, which were collected before the sporangia had begun to open, were washed in running water and brushed rather vigorously while in the water. They were dried on sterilized glass plates and the spores which were collected were sowed on various culture media. Cultures from material handled in this way contain few if any foreign prothallia. It is not difficult to tell by the appearance of a culture whether or not there are any foreign prothallia present, owing to differences in the rate of development and in the general habit of the prothallia of different species. It is fairly easy to distinguish between the

prothallia of the Polypodiaceae and the Cyatheaceae because of the differences in the antheridia and in the types of hairs.

From 2 to 15 cultures were made of all the species studied, the cultures running from 5 to 15 months. Various media were used: several different mixtures of soil; black peat, with and without Knop's solution; and porous clay crock standing in Knop's solution. Some of the cultures were raised in a laboratory where they received no direct sunlight except late in the afternoon; others were raised in a greenhouse where they received sunlight except for a few hours at midday.

The few cases of apogamy found occurred in the genera *Dicksonia* and *Cyathea*. They were found in cultures on peat raised in the greenhouse in the winter of 1915–1916. I am indebted to Professor A. VINCENT OSMUN of the Massachusetts Agricultural College for data on the weather of that winter and the 5 years preceding. While the total number of hours of sunlight for the winter of 1915–1916 was a little below the average, the number of days in which there was snow on the ground was considerably above the average, so that the greenhouse cultures of that winter probably received more light than any other set of cultures. LANG (8) regards intense light and probably high temperature as important factors in the development of apogamous structures. SCHLUMBERGER (10) found that in the case of *Woodsia ilvensis* the production of the cylindrical process was caused by such unfavorable conditions as weak light and dryness. HEILBRON (4) did not find dryness to be a factor and suggests that summer cultures are more likely to become apogamous than winter cultures, but his experiments with different qualities and intensities of light in moist cultures at a high temperature gave negative results. Mme. WORONIN is inclined to regard dryness as the cause of apogamy in the forms which she studied, as in these cases it cannot be attributed to intense light. This explanation is criticized by ISABURO-NAGAI (6), who found that in the case of *Asplenium Nidus* dryness was not a factor and that the cause seemed to be either an unfavorable culture condition or an unknown physiological condition. The cases discussed in the present paper are too few in number to be of much significance. It cannot be a question of dryness, as the cultures were on

moist peat. They were, however, exposed to rather intense light. It seems to be true that one explanation will not answer for all cases; the factors which cause apogamy in *Woodsia ilvensis*, a

FIGS. 1–3, 5.—*Dicksonia squarrosa:* fig. 1, prothallium with two apogamous buds, ×22; fig. 2, section through *a*, ×210; fig. 3, section through *b*, ×210; fig. 5, section of prothallium with archegonia and archegonial projections, ×90. Fig. 4, *Cyathea Tussacii:* archegonial projection, ×170.

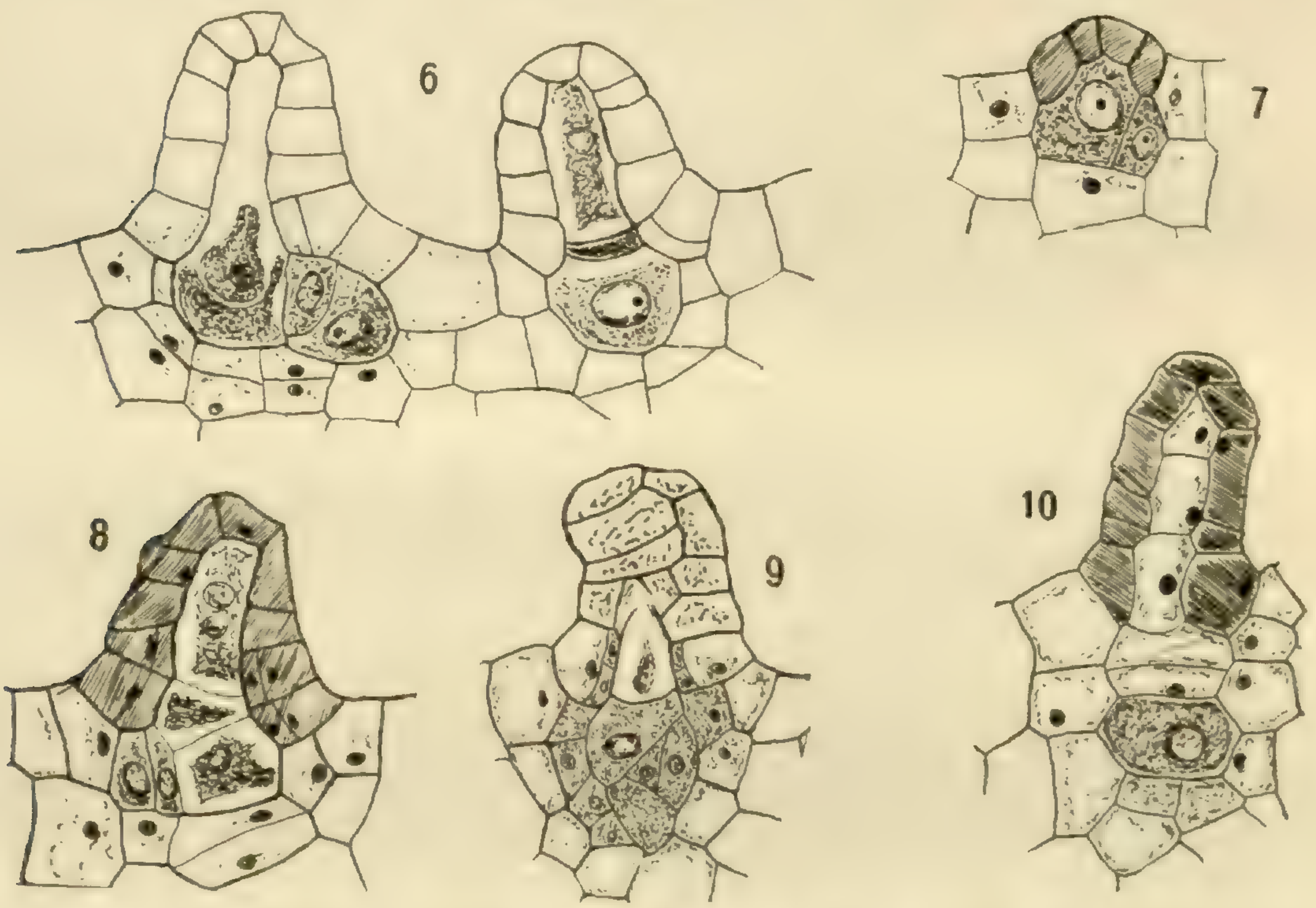
species which grows in exposed situations, are not necessarily the same as those which cause it in the species which grow in shaded places.

A convenient classification of types of apogamous development has been presented by FARMER and DIGBY (2), who begin their classification by distinguishing between premeiotic and postmeiotic apogamy. All the prothallia described in this paper were raised from spores, and accordingly the cases would be postmeiotic. The only case of obligate apogamy was found in a prothallium of *Dicksonia squarrosa* (Forst.) Sw. This prothallium had numerous antheridia and, although it was sufficiently large and had a well developed cushion, it had no archegonia. It produced two apogamous buds on the ventral side in the region where the archegonia usually appear (figs. 1, 2, 3). Behind one of the buds was a region where the thallus had thickened considerably and the outer cells had died. The presence of the characteristic cyatheoid antheridia makes it certain that this is not a polypod prothallium. Many prothallia of *D. squarrosa* showed the development of archegonial projections, such as HEIM (5) found on the prothallia of *Doodia caudata* and LANG found associated with apogamy in the species which he studied. Such projections are shown in figs. 4 and 5. *D. squarrosa* sometimes produced embryos as the result of fertilization, but these were not found on prothallia which had archegonial projections.

Cyathea muricata Wild. (*Alsophila muricata* Desv.) furnished the case shown in fig. 9. This may be the apogamous development of the oosphere, but it is quite as likely that it is the apogamous development of the ventral cell. Adjoining sections show that the archegonium had not opened. A nutritive region had begun to develop around the embryo. It will be noted that the shape and sequence of cell divisions are not the same as in the usual type of embryo.

In *Cyathea Tussacii* Desv. there were several cases of a peculiar behavior of the central cell. The first division does not cut off the primary neck cell, but instead cuts off a lateral cell (fig. 7). The central cell develops in the usual manner, while the lateral cell develops such structures as are seen in figs. 6 and 8. Such a division in the central cell was found also in *Dicksonia squarrosa* and a single case occurred in *Cibotium Schiedei* Schlecht. and Cham. *Cyathea Tussacii* and *Cibotium Schiedei* both produced archegonial

projections. In *Hemitelia horrida* (L.) R. Br. occurred the peculiar structure shown in fig. 10, an archegonium in which all the cells of the axial row except the egg have developed as vegetative tissue. The only development possible in this case would be an apogamous development. This species, however, showed no tendencies in that direction. It is impossible to say whether or not such structures as those shown in figs. 6, 7, 8, and 9 ever produce leafy



FIGS. 6–8.—*Cyathea Tussacii:* explanation in text, ×255; fig. 9, apogamous embryo of *Cyathea muricata*, ×255; fig. 10, peculiar archegonium of *Hemitelia horrida*, ×220.

sporophytes, as in a very short time it would be impossible to distinguish such an embryo from one produced as the result of fertilization. There was nothing in any of the material to indicate that these growths were ultimately checked, but the cultures did not continue long enough to show whether or not they would develop further. Neither species of *Cyathea* produced any embryos as a result of fertilization, although most of the archegonia appeared normal and the sperms were active, many being found in archegonia.

MOUNT HOLYOKE COLLEGE
SOUTH HADLEY, MASS.

LITERATURE CITED

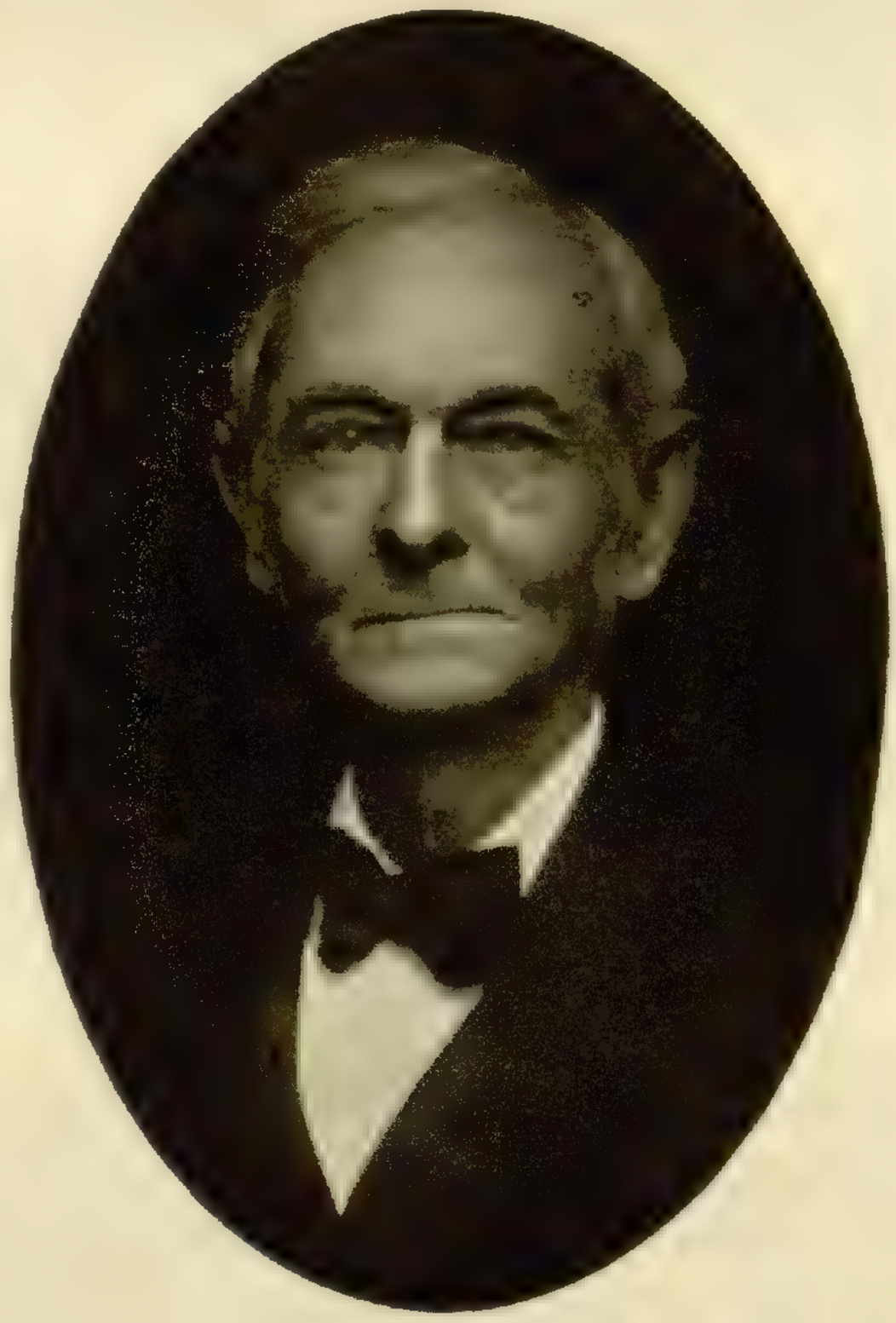
1. BOWER, F. O., On some normal and abnormal developments of the oophyte in *Trichomanes*. Ann. Botany **1**:269–305. *pls. 14–16*. 1888.
2. FARMER, J. B., and DIGBY, L., Studies in apospory and apogamy in ferns. Ann. Botany **21**:161–199. *pls. 16–20*. 1907.
3. FARLOW, W. G., Über ungeschlechtliche Erzeugung von Keimpflanzen auf Farnprothallien. Bot. Zeit. **32**:180–183. 1874.
4. HEILBRON, ALFRED, Apogamie, Bastardierung, und Erblichskeitverhältnisse bei einigen Farnen. Flora **101**:1–42. *figs. 43*. 1910.
5. HEIM, C., Untersuchungen über Farnprothallien. Flora **86**:329–373. *figs. 16*. 1896.
6. ISABURO-NAGAI, Physiologische Untersuchungen über Farnprothallien. Flora **106**:281–330. *figs. 18*. 1914.
7. LEITGEB, H., Die Sprossbildung an apogamen Farnprothallien. Ber. Deutsch. Bot. Gesell. **3**:169–176. 1885.
8. LANG, W. H., On apogamy and the development of sporangia upon fern prothallia. Phil. Trans. Roy. Soc. London B **190**:189–238. *pls. 7–11*. 1898.
9. SADEBECK, R., Schenck's Handbuch der Botanik. **1**:233. 1879.
10. SCHLUMBERGER, O., Familienmerkmale der Cyatheaceen und Polypodiaceen und die Beziehung der Gattung *Woodsia* und verwandter Arten zu beiden Familien. Flora **102**:383–414. *figs. 15*. 1911.
11. SHAW, W. R., Parthenogenesis in *Marsilia*. BOT. GAZ. **24**:114–117. 1897.
12. STANGE, F. T., Mittheilungen über seinen Farnculturen und die bei denselben beobachtete Apogamie. Sitz. Gesell. Bot. Hamburg. 1886.
13. STRASBURGER, E., Apogamie bei *Marsilia*. Flora **97**:123–191. *pls. 3–8*. 1907.
14. WORONIN, HELENE, Apogamie und Aposporie bei einigen Farnen. Flora **98**:101–162. *figs. 72*. 1908.

BRIEFER ARTICLES

CHARLES HORTON PECK

(WITH PORTRAITS)

Dr. CHARLES HORTON PECK, for many years Botanist of New York State, died at his home in Menands, New York, on July 11, 1917. He suffered a light stroke early in November 1912. A severe one in the spring of 1913 rendered him incapable of further work. Soon after this he presented his resignation as State Botanist, but it was not accepted by the Regents of the University of the State of New York until January 26, 1915. A testimonial minute was recorded at the time by the Regents, citing Dr. PECK's valuable services to the state and to science by his conscientious and untiring labors. Dr. PECK was greatly depressed early in 1912 by the death of his wife, and by the news that the herbarium would have to be moved from the Old Agricultural Hall to the new quarters in the State Education Building.



He was born at Sand Lake (now called Averill Park), New York, March 30, 1833. He graduated from the State Normal School at Albany in 1852. He then taught for three years in Schram's Collegiate Institute at Sand Lake. He entered Union College, Schenectady, in 1855, and graduated in 1859. He resumed his teaching at the Collegiate Institute in Sand Lake for three or four years. In 1862 or 1863 he was appointed teacher of Latin and Greek in the Albany Classical Institute, known more popularly as Cass's Institute, as it was presided over by AMOS CASS.

Here Dr. PECK is said to have become "an accomplished classical scholar, but his real interest lay all the time in the world of plants and flowers" (The Knickerbocker Press, Albany, July 12, 1917). It is evident, therefore, that for some time Dr. PECK had been engaged in the collection and study of plants. It may be a matter of interest to botanists to know the circumstance which first aroused his interest in botanical investigation which was so soon to supersede his interest in the classics. On two different occasions the writer had the opportunity of collecting and studying fungi for a week with Dr. PECK, first in the Adirondack

Mountains at Lake Piseco in 1902, and then at Port Jefferson, Long Island, in 1904. While at Lake Piseco Dr. PECK told the writer of the first impulse he received in the direction of the study of the lower plants. It was while teaching school at Sand Lake (probably in Schram's Collegiate Institute). One of his duties in those days appears to have been to help keep up the fire. While putting wood into the stove he was constantly attracted by the lichens and mosses growing on the bark. This gave him a desire to know something about the mosses. He got into communication with several students of the mosses at that time, probably LESQUEREUX[1] first, and later with C. F. AUSTIN.

[1] Rept. N.Y. State Cab. Nat. Hist. **19**:42. 1866.

Dr. PECK states[2] that ELLIOT C. HOWE, while at Fort Edwards, directed his attention to the study of the fungi and induced him to take up this field of investigation. He told the writer that he was advised to correspond with M. C. COOKE[3] of London concerning the fungi. This relation with COOKE is shown by the large number of new species of fungi published by PECK, in his early work, ascribed to COOKE and PECK. It appears that he received assistance in the determination of fungi from M. A. CURTIS before he became associated with COOKE. The first new species published by him was "*Septoria viridetingens* Curtis in litt.," in the 23d Rept. 55, 1873,[4] PECK being completely responsible for the diagnosis. He was, therefore, in correspondence with CURTIS at least as early as 1869, and probably earlier. During this period he was in correspondence also with other early students of the fungi, RAVE, PETERS, MICHENER, GERARD, FROST, and the Rev. J. BLAKE in this country. He had an extensive correspondence and exchange of specimens, not only with COOKE, but with other European mycologists, as DE THÜMEN, ROUMEGUÉRE, and others. Dr. PECK told the writer that he was advised to correspond with M. C. COOKE.

In the 18th Report (for 1864) of the Regents of the State of New York there is a catalogue of the mosses which were presented to the State Museum by Dr. PECK (pp. 193–196, 1864). In the 19th Report (for 1865, pp. 42–70, 1866) there is a list of the mosses of the state of New York by him. In the 20th Report (for 1866) there is an article by

[2] Bull Torr. Bot. Club **26**:253. 1899.

[3] I have since forgotten the name of the person who made the recommendation, but it was one of three persons: E. C. HOWE, who had relations with the Rev. M. C. CURTIS of North Carolina, CURTIS himself, or the Rev. E. C. BOLLES, a Universalist clergyman of Salem, Massachusetts. Dr. FARLOW informs me that BOLLES, in the early seventies, was a well known popular lecturer on botany and zoology, and a great admirer of COOKE, who sent him many colored drawings and pamphlets on fungi. As BOLLES traveled about the country a great deal, he may have met CHARLES PECK; but the weight of evidence seems to indicate HOWE or CURTIS as the one who suggested COOKE to him. In this connection I wish to express my obligations to Dr. W. G. FARLOW, Mrs. E. G. BRITTON, Dr. H. D. HOUSE, the present State Botanist, and Mr. HARRY S. PECK, whom I recently met in Albany, for assistance in obtaining some of this information.

[4] This was the report for 1869, transmitted to the legislature March 10, 1870. In a letter to the writer, December 14, 1912, Dr. PECK stated that "the 23rd Report was published in 1873 as stated therein. A fire in the publishing house of Weed Parsons and Co. delayed the publication of the 23rd, so that the 24th got ahead of it." It is stated by some, however, that a separate of the botanical 23d Report was published in 1872.

him on "Facts and observations touching the flora of the state of New York" (pp. 403–410, 1867). This indicates that he was in touch with the scientific work of the Museum (then the State Cabinet of Natural History) before his appointment to the staff, and evidently enjoyed a close acquaintance with one of the Regents, himself a botanist, G. W. CLINTON, of Buffalo. He was appointed Botanist of the Museum in 1867. In 1883 the legislature created the position of State Botanist, to which Dr. PECK was appointed and which he held until his retirement in 1915.

He was most celebrated for his taxonomic studies and publications on the fungi, although seed plants, ferns, and mosses received considerable attention in nearly all of his reports, and quite a number of new species of seed plants were described by him. His activities in this field were not confined to New York State. He had many correspondents from all parts of the United States and Canada. His reports as State Botanist began with the 21st Museum Report for 1867 (published in 1868), and the last one by him was the Museum Report for 1912 (Bulletin 167, 1913). These reports have carried the name and work of Dr. PECK to all parts of the scientific world. With few exceptions the new species of fungi described in these reports included only those from New York State. Some of the early ones were published in the *Bulletin of the Buffalo Society of Natural History* and in the *Transactions of the Albany Institute of Arts and Sciences*. New species from territory outside of the state were mostly published in his numerous contributions to the BOTANICAL GAZETTE and to the *Bulletin of the Torrey Botanical Club*, dating from the very early history of these journals. His work covered all the groups of the fungi, and the new species described by him number between 2000 and 3000. A list of those published up to 1908 is given in the Museum Bulletin no. 131, pp. 59–190, 1909. These reports of the State Botanist have been in great demand by students of fungi, especially because there had been no manual of the fungi of North America.

The monographs of certain genera of the agarics form a very valuable feature of his work, particularly those appearing in a number of his later reports. His monograph of the Boleti of the United States (N.Y. State Mus. Bull. no. 8, 1889) should also be mentioned. He gave considerable attention to testing the edible properties of the fleshy fungi, as several of his reports testify. It is unfortunate that he was not able to complete monographs of all the genera of the agarics. During the

later years of his activity considerable time was given to study and collecting the Crataegi of the state for the State Herbarium.

Dr. PECK possessed a very critical and analytical mind. Many of his descriptions of new species are marvels of accuracy and clearness. On the two occasions when I had the opportunity of working with him in the field I was impressed by these qualities manifested in a marked degree. Each day he made a careful study of his collections, with full notes and often accompanied by colored drawings, from which were selected those for color reproduction in his reports. The photograph presented here, showing him at work, was made by the writer in his room at the hotel in Port Jefferson in 1904. On the table are some of the fungi, his water color blocks, and a color chart made by himself which he used for many years. Perhaps in some respects he was, at times, too critical, which may have led him to distinguish as different species environmental and growth forms of the same species, but in this respect he did not differ from most other taxonomists. This faculty, however, may be regarded as a virtue compared with the careless "lumping" so characteristic of some students who have taken a plunge into monographic work in the fungi without an adequate background of critical studies of the morphology and structure of the fleshy fungi in a fresh state. That a number of European species have been described by PECK (and others) as new is not surprising when we consider the poor and meager descriptions which appeared in the earlier, and some modern, European works on mycology.

This leads the writer to mention some of the other difficulties under which Dr. PECK labored. There has been a lamentable lack of proper equipment in apparatus, exsiccati, and of assistance in the Botanical Division of the State Museum, not to mention the very inadequate rooms and space which were assigned to the State Botanist. The latter feature has been vastly improved in the botanical quarters in the new Education Building, although even now there is no room suitably lighted for microscopic work. Dr. PECK, through nearly all the 48 years of his official connection with the Museum, worked single-handed and alone, carrying on his vast correspondence by hand, and caring as best he could for the large number of specimens collected by himself and communicated by his correspondents. Partly for this reason, and partly due to the fact that when the botanist's quarters were moved to the attic of the Capitol Building, most of the collections, for want of room, were bundled up and almost inaccessible; the collections

for a number of years were in a very chaotic state. When they were moved to the Agricultural Hall, some order began to come out of this chaos, and further improvement was introduced when an assistant (S. H. BURNHAM) was appointed. The present State Botanist, Dr. H. D. HOUSE, still has but one assistant. Nevertheless, the collections are being arranged in a more orderly manner; many of the types have been marked, and all are more accessible to students. For the care of this very valuable collection, and for the continuance and upbuilding of the botanical interests of the State Museum, New York should be more generous than it has been thus far.

Dr. PECK was a life member of the Botanical Society of America, a Fellow of the American Association for the Advancement of Science, member of the American Forestry Association, of the Albany Institute of Arts and Science, of the National Geographic Society, of the Torrey Botanical Club, and an honorary member of the New England Botanical Club.

The state and mycological science owe Dr. PECK a fund of gratitude for what he has accomplished in spite of the many difficulties and discouragements under which he labored. This recognition of his labors has been partly made by a testimonial to him, in the shape of a collection of colored models of some of the more important large fungi, which is displayed in the main museum room on the fifth floor of the Education Building.—GEO. F. ATKINSON, *Cornell University*.

A NEW POISONOUS MUSHROOM

(WITH THREE FIGURES)

The genus *Clitocybe* is a large one, with approximately 400 species. Very few of this large number are known to be poisonous or deleterious in other ways when eaten. Among these may be mentioned from North

FIG. 1.—*C. acromelalga* growing on ground in bamboo forest

America the phosphorescent species *C. illudens* Schw., which produces serious nausea, and *C. sudorifica* Pk., which, eaten in small quantities, causes a "profuse perspiration sometimes continuing for 5 or 6 hours" (N.Y. State Mus. Bull. no. 157. 68. 1912), but is "sufficiently toxic to cause the death of frogs, rabbits, and guinea pigs." It is a matter of

interest, therefore, to record the discovery of another poisonous species of this genus, which is also a hitherto undescribed one. It was found growing on the ground among other vegetation in a bamboo forest in Tsurugiji, Noto, Japan. The poisonous effects from eating this mushroom are manifested by an acute burning pain in the fingers and toes within 3 days. The pain is mitigated by placing the hands and feet in running water.

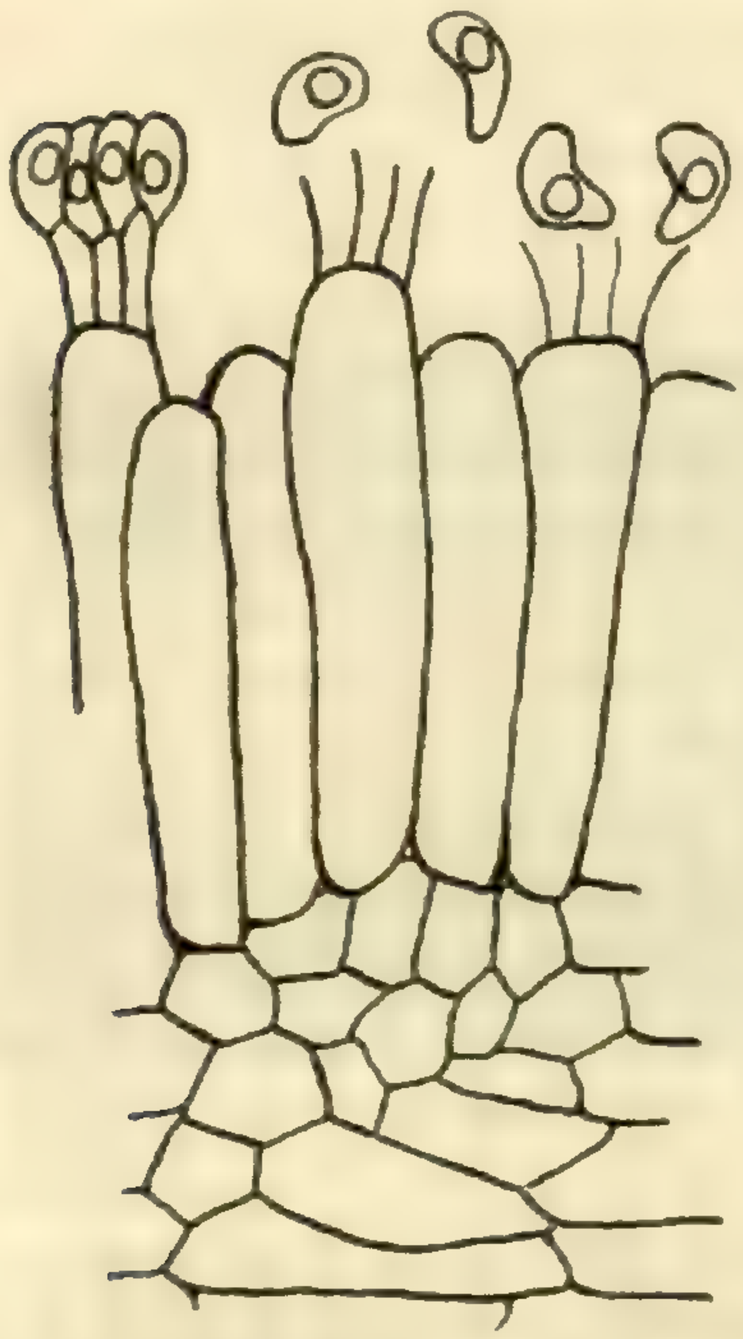


FIG. 2.—Basidiospores of *C. acromelalga;* ×1500.

Clitocybe acromelalga, n. sp.—Plants 3–6 cm. high; pileus 5–10 cm. broad, orange yellow when fresh, dark brown red when dry, subfleshy and pliant, depressed, margin incurved when young, splitting in age, surface smooth, flesh white; lamellae white, crowded, thin, slightly decurrent; basidia 4-spored; spores white, smooth, oboval, 3–4×1.5–2.5μ; stem rigid, fibrous, hollow, concolorous with the pileus, 2–5 cm. long, 0.5–1 cm. thick.—Odor and taste not marked. Poisonous effects, *acromelalga.* October to November, on the ground in a bamboo forest, Tsurugiji, Noto, Japan.—T. ICHIMURA, *Kanazawa, Japan.*

FIG. 3.—*Clitocybe acromelalga*; $\times \frac{2}{3}$

CURRENT LITERATURE

NOTES FOR STUDENTS

Physiology of fungi.—The increasing attraction of this subject is evidenced by the number of papers that have appeared recently. The Graduate Laboratory of the Missouri Botanical Garden is publishing a series of such papers, 4 of which are noted herewith.

DUGGAR and DAVIS[1] deal with the often investigated problem of nitrogen fixation. Using a method by which the fungi were grown, digested, and distilled in the same flask without transfer, they were unable to demonstrate nitrogen fixation by *Aspergillus niger*, *Macrosporium commune*, *Penicillium digitatum*, *P. expansum*, and *Glomerella Gossypii*. In cultures of *Phoma Betae* on mangel and on sugar beet decoction with sugar, a nitrogen gain of 3.022–7.752 mg. was established, which they take to be a definite proof of fixation. A good review of the literature is included.

ZELLER[2] reports the following enzymes as occurring in a specially prepared enzyme powder from the wood destroying fungus *Lenzites saepiaria*: esterases, maltase, invertase, raffinase, emulsin, tarmase, diastase, inulanase, ligninase, cellulase, hemicellulase, pectinase, urease, hippuricase, nuclease, proteinase (both tryptic and ereptic), rennetase, oxidase, and catalase. Pectase and lactase were not demonstrated, and only slight indications were found of the presence of amidase. A comparative study of the enzymes occurring in sporophoral and mycelial tissue showed that the important metabolic processes are carried on in the latter.

ZELLER[3] also deals with the physical properties of wood in relation to decay. On the basis of an extensive series of tests, he concludes, contrary to the opinion of other workers in this field, that resin is no safe index of the durability of the 3 species of yellow pine investigated. If it increases durability at all, it does so more by its waterproofing effect than by the toxic effect on the growth of fungi sometimes claimed for it. As a more reliable and practical

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[1] DUGGAR, B. M., and DAVIS, A. R., Studies in the physiology of the fungi. I. Nitrogen fixation. Ann. Mo. Bot. Gard. **3**:413–417. 1916.

[2] ZELLER, S. M., Studies in the physiology of the fungi. II. *Lenzites saepiaria* Fries., with special reference to enzyme activity. Ann. Mo. Bot. Gard. **3**:439–512. 1916.

[3] ———, Studies in the physiology of the fungi. III. Physical properties of wood in relation to decay by *Lenzites saepiaria*. Ann. Mo. Bot. Gard. **4**:93–164. 1917.

criterion of durability, he recommends specific gravity, which, he says, is easily determined by inspection. The points to be noted are the proportion of summer wood to spring wood in the growth rings, and the width of the growth rings. If these are narrow, if the proportion of summer wood is high, and if the proportion of sap wood is low, the piece of pine can be considered of high specific gravity and therefore durable.

DUGGAR, SEVERY, and SCHMITZ[4] have made a study of the growth of *Macrosporium commune*, *Aspergillus niger*, *Glomerella* (*Gloeosporium*) *Gossypii*, and *Penicillium expansum* on decoctions made from green string beans, corn meal, fresh turnips, sugar beets, dried prunes (exclusive of seed), and potatoes. Besides the natural decoctions, variants of these were used, containing, in addition to the plant extracts, different amounts of acid or alkali, cane sugar, potassium nitrate, and potassium acid phosphate. They found that the addition of sugar, nitrate, and phosphate gave in every case except one (*Glomerella* on bean decoction) increase in growth over the addition of sugar alone. Usually the next highest growth occurred when sugar and nitrate were added. Sugar alone gave a relatively slight increase over the natural decoction. The prune decoction seemed less favorable for growth than any of the others, except in the case of *Macrosporium*. Hydrogen-ion determinations, made by the colorimetric method, showed that in all solutions except the sugar beet and the corn meal decoctions *Aspergillus* caused a shift toward the acid side usually about 10^{-3}, while *Macrosporium* and *Glomerella* generally caused a pronounced shift in the other direction. It is worthy of note here that REED[5] found an increase in alkalinity in cultures of *Glomerella rufomaculans*, while the writer[6] has shown the same condition to hold in case of apple bark attacked by blister canker (*Nummularia discreta*). *Penicillium* caused an increase in acidity in the natural and standardized decoctions.

From the results of an investigation of the mosaic diseases of plants, FREIBERG[7] comes to the conclusion that the infectious substance is an enzyme and not a virus, as ALLARD claims to have shown in recent work on the mosaic disease of tobacco. FREIBERG'S reasons for his conclusion are that the infective principle is adsorbed by talc, and is destroyed by concentrations of alcohol and by temperatures which are destructive to enzymes. The fact that the infective principle is destroyed by formaldehyde is due, he thinks, to a specificity

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[4] DUGGAR, B. M., SEVERY, J. W., and SCHMITZ, H., Studies in the physiology of the fungi. IV. The growth of certain fungi in plant decoctions. Ann. Mo. Bot. Gard. **4**:165–173. 1917.

[5] REED, H. S., The enzyme activities involved in certain fruit diseases. Va. Exp. Sta. Rept. 1911–1912 (pp. 51–78).

[6] ROSE, D. H., Oxidation in healthy and diseased apple bark. BOT. GAZ. **60**:55–65. 1915, and unpublished work.

[7] FREIBERG, G. W., Studies in the mosaic diseases of plants. Ann. Mo. Bot. Gard. **4**:175–232. 1917.

of reaction between the two and not to the antiseptic properties of the formaldehyde. This explanation he finds further supported by the fact that the infective power of extracts from diseased plants is not destroyed by treatment for two days with concentrated solutions of ether, chloroform, carbon tetrachloride, toluene, acetone, and glycerine. In this connection it is well to remember a statement by SMITH[8] that in a number of organisms tested by him 10 grew in the presence of chloroform (5 cc. of chloroform in test tubes with 10 cc. of milk or beef bouillon), and 2 grew vigorously in the presence of thymol. He further states that, "in the opinion of the writer, statements of physiologists respecting the existence of enzymes in the tissues and fluids of higher plants must be taken with much allowance when chloroform, thymol, and similar antiseptics have been depended upon to keep the solution free from bacteria. A medium to which chloroform or thymol has been added must be shut in and shaken continuously if the full antiseptic value of these substances is to be obtained."

Microchemical tests showed starch and sugar present in greater amounts in the dark green than in the chlorotic areas. FREIBERG suggests that this condition, taken in connection with the specificity of reaction between formaldehyde and the infective principle, and the possibility that formaldehyde is one of the first products of photosynthesis, may form a basis upon which the physiological nature of mosaic diseases may be explained. The possible relation of these factors to the formation of an enzyme is not made clear. Neither is it made clear how an enzyme can "reproduce itself." If it does so, why is not ALLARD'S contention the better one, that the causal agent is an organism and not an enzyme? And if it be granted for the sake of argument that the blotching of the leaves is caused by an enzyme, the question of the origin of the enzyme is still unanswered. In the work of ABERHALDEN and of KNUDSON, cited by FREIBERG, the development of proteolytic enzymes or of tannase was not spontaneous, but resulted from a stimulus foreign to the organism.

Yellows or wilt, a serious disease of cabbage in many parts of the country, has recently been investigated by Gillman.[9] He finds that the causal fungus, *Fusarium conglutinans* Wollenw., has a high optimum temperature and is very resistant to drying, both in pure culture and in the soil. The characteristic symptoms of the diseases are dependent on a temperature of about 17–22° C. or above for their occurrence. Lower temperatures (12–16° C.) under controlled conditions prevented the occurrence of the trouble in the greenhouse.

Two rusts of economic importance, *Puccinia coronata* Cda. and *P. Sorghi* Schw., are the subject of a physiological investigation by MAINS.[10] The

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[8] SMITH, E. F., Bacteria in relation to plant diseases. Ann. Mo. Bot. Gard. 1:74, 75. 1905.

[9] GILLMAN, JOSEPH C., Cabbage yellows and the relation of temperature to its occurrence. Ann. Mo. Bot. Gard. 3:25–84. 1916.

[10] MAINS, E. B., The relation of some rusts to the physiology of their hosts. Amer. Jour. Botany 4:179–221. 1917.

optimum temperature for the former is put at about 20° C., for the latter 30°. The fact that no injury appears in the infected cells, but only in the cells surrounding them, is thought by MAINS to be due to starvation brought about by withdrawal of foods to the infected region. It is possible, however, that the injury might be caused by injurious enzymes or other toxic substances which diffuse outward from the infected cells. The growth of the rusts and the development of spore pustules were increased when some carbohydrate was added to the nutrient solution, and the conclusion is drawn that "the obligate parasitism of the rusts is probably explained by their requirement of some transitory or nascent organic products related to the carbohydrates which they obtain in the living plant." This conclusion is hardly in accord with the statement made by RUSSELL[11] that wheat plants whose photosynthetic activity has been seriously decreased by lack of potash, and whose carbohydrate content is therefore low, are especially susceptible to attacks of rust. Further work seems necessary to clear up the situation.

BROOKS and COOLEY[12] find that in inoculations on apples all of the fungi tested grew at 0° C. except *Fusarium radicicola* and *Glomerella cingulata*, the former making no growth at 15° and the latter none at 10°. *Sphaeropsis malorum* had produced no evident rot at 15° by the end of a week, the species of *Penicillium* and *Neofabraea* at 10° by the end of two weeks, while *Sclerotinia cinerea* produced measurable rots at 5° in one week and at 0° in two weeks. *Neofabraea malicorticis* had an optimum at 20°, *Fusarium radicicola* at 30°, and all the other fungi at 25°. When grown on corn meal agar in Petri dishes, all the fungi showed the same optimum and maximum as in the fruit inoculation experiments. With most of the fungi the initial incubational stages of growth on the fruit were more inhibited by low temperatures than the later ones. The results of the investigation show the importance of immediate as compared with delayed storage; the value of temperatures of 5 or 10° in short periods of storage, and of 0° in longer ones; and further that the minimum temperature varies with the prevalent fungus and with the variety and maturity of the fruit.

In an investigation of the growth of fungi on nutrient solutions by HAWKINS[13] it was found that *Aspergillus niger*, *Penicillium glaucum*, and *Botrytis cinerea* grew readily in solutions of potassium and calcium nitrate, sucrose, and glucose in which the diffusion tensions were much higher than the total diffusion tensions of the dissolved substances in the juices of their host plants.—D. H. ROSE.

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[11] RUSSELL, E. J., Soil conditions and plant growth. 2d ed. London. 1915 (pp. 41, 42).

[12] BROOKS, CHARLES, and COOLEY, J. S., The temperature relations of apple-rot fungi. Jour. Agric. Research 8:139–163. 1917.

[13] HAWKINS, LON A., Growth of parasitic fungi in concentrated solutions. Jour. Agric. Research 7:255–260. 1916.

Endemism.—RIDLEY[14] recently presented a series of criticisms of the work of WILLIS on endemism in Ceylon. WILLIS had attempted to demonstrate by the statistical method that endemics were the most recent rather than the most ancient forms in a given locality. In his criticism RIDLEY objected that the statistics used were inaccurate, pointing out a number of flaws. In addition he presented from his own experience some striking exceptions to the general conclusion of WILLIS. In conclusion, RIDLEY objected to the use WILLIS had made of the mutation theory, RIDLEY himself evidently being a confirmed natural selectionist.

WILLIS[15] has now answered these criticisms in a rather satisfactory way. As to the flaws in his statistics, he points out how they are quantitatively of little significance. As to the applicability of his conclusions, he presents two crucial cases: (1) showing that the widely distributed forms of New Zealand "take no notice" in their distribution of Cook's Strait (of relatively recent origin), while the endemics do; (2) the "local distribution of the highly modified Tristichaceae and Podostemaceae and the cosmopolitan distribution of the little modified forms." As to man's action, changes of climate, and similar disturbing factors which RIDLEY had accused him of neglecting, WILLIS stated that these, although they may exert a disturbing influence, no more affect the validity of his law than does the resistance of air effect the law of gravity. Finally, WILLIS deals with RIDLEY'S theoretical objections merely by pointing out that natural selection cannot explain the origin of the peculiarities which distinguish plants, but can only preserve or destroy them when once formed.

In an accompanying paper SINNOTT[16] raises additional objections to the hypothesis of WILLIS. He says that "other factors than age determine the area occupied by a species." He can hardly claim, however, that this affects the validity of the law. He also states that the data of WILLIS would seem to indicate that woody plants are producing new species faster than are herbs, a conclusion against which there is much evidence; and likewise they would indicate that herbs are the older since they are the more widely distributed. BAILEY and SINNOTT had previously stated and substantiated the contrary view. May not the two ideas be reconciled, however, by the fact that it is the nature of herbs to spread the more rapidly, due to more meager requirements for germination and to more extensive vegetative multiplication? SINNOTT also states that species *are* dying out, due to actual extermination, "which causes the last survivors to appear as 'relic' endemics"; and by "swamping" of isolated members of old species by crossing with newly devel-

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[14] Rev. in BOT. GAZ. **64**:263. 1917.

[15] WILLIS, J. C., The relative age of endemic species and other controversial points. Ann. Botany **31**:189–208. 1917.

[16] SINNOTT, EDMUND W., The "age and area" hypothesis and the problem of endemism. Ann. Botany **31**:209–216. 1917.

oped forms. WILLIS had concluded that species are *not* dying out. In conclusion, SINNOTT emphasizes the complexity of the problem and points out the many factors involved. The complexity of a problem, however, should justify rather than discourage the development of such a theory.—MERLE C. COULTER.

Free ammonia and ammonium salts in plants.—WEEVERS[17] has made a large number of determinations for free ammonia and ammonium salts in tissues of various members of the plant kingdom. Tests for ammonium salts were made as follows: a portion of the plant material (25 mg.) along with a drop of water was placed in the bottom of a collared microscope slide. Some powdered magnesia and a wad of cotton bearing a little chloroform were added. A cover glass bearing a hanging drop of platinic chloride was then placed on the collar. The chloroform killed and rendered the cells permeable, while the magnesium oxide liberated the ammonia from the ammonium salt of the tissues. The ammonia was detected by the $(NH_4)_2Pt\ Cl_6$ crystals in the hanging drop. For the detection of free ammonia only the tissue or the tissue and the chloroform were added along with the hanging drop. Sodium hydrate (20 per cent) could be substituted for magnesia only in case the reaction was rapid, for the former liberates ammonia from amides in a few hours at room temperature. WEEVERS believes he could estimate closely the relative amount of ammonium salts in various tissues by the amount of $(NH_4)_2Pt\ Cl_6$ crystals formed. His estimates tallied with the quantitative determinations that were made in many cases.

Among phanerogams free ammonia was found only in bacterial nodules. In cryptogams it was occasionally found in Hymenomycetes and lichens. Ammonium salts were found in all species examined except in some mycotropic and insectivorous forms naturally growing on acid moorlands poor in ammonium salts. Their absence in these forms is apparently related to the nature of their protein metabolism and not to nitrogen shortage in the soil, as indicated by their behavior in water cultures and by other plants of the same habitat bearing ammonium salts. The amount of ammonium salts present in the leaves of any plant is apparently independent of their presence in the soil. Ammonium salts that are absorbed by the roots from water cultures are quickly transformed and do not influence the amount in the leaves. Many facts indicate that these salts result from protein metabolism, assimilation, and dissimilation. The more vigorous metabolism in any part the more ammonium salts are present. Some plants and plant parts are rather rich in ammonium salts, bearing as much as 2 per cent; certain sea forms (*Noctiluca miliaris*); many hymenomycetes and lichens (excepting lichens on moorlands); certain Liliaceae and Cruciferae (onion and cabbage roots), and root nodules of

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[17] WEEVERS, TH., Das Vorkommen des Ammoniaks und der Ammonsalze an den Pflanzen. Rec. Trav. Bot. Neerland. **13**:63–104. 1916.

Papilionaceae. The author believes that certain of the mycotropic forms are limited to acid soils because of the use, through the help of their mycorrhiza, of organic nitrogen compounds, and these are most abundant in absence of lime. —WM. CROCKER.

Hybrids of maize.—COLLINS[18] makes a contribution to the genetics of maize by reporting results from his studies of hybrids between pod corn and a type discovered by Dr. W. B. GERNERT, in which the pistillate inflorescence is replaced by a compound inflorescence branched as is ordinarily the case with the tassel.

In his experiments the progeny of ordinary *tunicata* plants has always consisted of approximately 3 tunicates to 1 normal. In other words, the usual tunicate ear is a heterozygous dominant. The homozygous dominant is apparently a type which makes up about one-third of the total number of tunicate plants and is characterized by greatly enlarged tassels containing both staminate and pistillate flowers, and the ear either with enlarged sterile spikelets or wanting. *Zea ramosa*, on the other hand, is recessive to normal.

In 1914 a cross was made between half-tunicate (heterozygous) ♂ and *Zea ramosa* ♀. Of 9 first generation plants, 4 were tunicate and 5 normal, the tunicate ears being "half-tunicate" and showing no trace of *ramosa* characters. From 2 selfed F_1 non-tunicate ears 85 plants were raised, of which 65 were normal and 17 *ramosa*. From 3 selfed F_1 half-tunicate ears 326 plants matured. Among the *tunicata* plants of this lot there were both *tunicata* and *ramosa* tassels, and in the latter a new type appeared which had indeterminately branched inflorescences embryonic in nature. This peculiar type (termed cauliflower) occurred in both lateral and terminal inflorescences, although more common in the former. A simple Mendelian interpretation of these results is given.—E. M. EAST.

A New Zealand biological station.—Canterbury College has recently set apart a tract of land in the mountainous center of South Island, New Zealand, and provided it with buildings suitable for a biological station. It is situated at an altitude of 1850 ft. on the Cass River and is surrounded by mountains, some of which are over 5000 ft. high. Descriptions of its situation,[19] its physiography,[20] and its vegetation[21] seem to show that it is well suited to the purpose for which it was intended. The vegetation displays a wide

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[18] COLLINS, G. N., Hybrids of *Zea ramosa* and *Z. tunicata*. Jour. Agric. Research **9**:383–395. *pls. 13–21.*

[19] CHILTON, CHAS., Introduction and general description of station. Trans. New Zealand Inst. **47**:331–335. 1915.

[20] SPEIGHT, R., The physiography of the Cass district. *Ibid.* **48**:145–153. 1916.

[21] COCKAYNE, L., The principal plant associations in the immediate vicinity of the station. *Ibid.* **48**:166–186. 1916.

diversity of types, including bits of forests of the southern beech, *Nothofagus Cliffortioides*, various scrub associations, and low tussock grassland, with transitions through reed and sedge swamp to open water. Of these the tussock grassland is by far the most important and interesting, representing as it does a montane association covering some 6,000,000 acres ranging from an altitude of 1000 to 3000 ft. It is dominated by the two smaller tussock grasses, *Poa caespitosa* and *Festuca nova-zealandiae*, in many places changed by burning and sheep grazing so as to permit the invasion of other grasses and herbs. The association not only presents many interesting ecological problems, but its proper utilization is a matter of great economic importance,[22] since one-seventh of the occupied land of New Zealand is covered with this vegetation. At present it is largely given over to sheep grazing, but without producing satisfactory returns.—GEO. D. FULLER.

Anatomy of Gnetum moluccense.—LA RIVIÈRE[23] has described the structure of a single branch of *Gnetum moluccense*. The greater part of the paper is devoted to a study of the accessory (secondary) steles outside of and concentric with the first stele. The remarkable conclusion is reached that they originate in the nodes from ramifications of bundles passing to the lateral branches and then grow *downward* (toward the base of the stem), the cambiums appearing at lower and lower levels in the inner cortex. The difficulties in this conception, that the direction of their growth is the reverse of the usual one, will present themselves to both morphologists and physiologists. Communications of the accessory steles with each other and with the central one, originally discovered by BERTRAND but overlooked by all later workers, are carefully traced and appear to be quite numerous. The different tissues of the whole stem are briefly described, but according to the author's observations present no features of outstanding morphological significance. This is perhaps the reason that no conclusions are mentioned in regard to the affinities of Gnetales with either gymnosperms or angiosperms.—W. P. THOMPSON.

Nitrogen determination.—Several years ago FOLIN modified the Kjeldahl method of determining nitrogen so that small quantities could be determined with sufficient accuracy. DAVIS,[24] who has used this modified method extensively for determination of nitrogen in small quantities of plant materials, reports that it is specially good for demonstrating proteolytic changes, for determination of nitrogen in minute plant sections or organs, and the effects of various factors upon the nitrogen content of plant tissues. The method is

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[22] COCKAYNE, A. H., Some economic considerations concerning montane tussock grassland. *Ibid.* **48**:154–165. 1916.

[23] LA RIVIÈRE, HENRIETTE C. C., Sur l'anatomie et l'epaississement des tiges du *Gnetum moluccense* Karst. Ann. Jard. Bot. Buitenzorg **30**:32–58. *pls. 4–12*. 1916.

[24] DAVIS, A. R., A note on the adaptability of the Folin micro-Kjeldahl apparatus for plant work. Ann. Mo. Bot. Gard. **2**:407–412. 1916.

best suited to amounts of nitrogen running from 0.5 to 5 mg., and the substance taken for determination should correspond to such quantities of nitrogen. The apparatus consists of small Kjeldahl flasks, fume absorbers, micro-burners, Ostwald pipettes, and small condensers, all readily obtainable or easily constructed. Titration is used, rather than the colorimeter method, for the actual determination. A comparison of the determinations with the micro- and macro-Kjeldahl method shows that the micro method can be relied upon as reasonably accurate. The method will be exceedingly valuable with advanced classes in physiology.—CHARLES A. SHULL.

Carbon nutrition.—The ability of *Glomerella cingulata* to utilize certain pentosans and pentoses as a source of carbon has been investigated by HAWKINS.[25] He finds that arabin and xylan, and the derived sugars, arabinose and xylose, may be used as the sole source of carbon. When this fungus causes rot in apples, it decreases the total furfurol-yielding content of the apple, but the alcohol-soluble portion of the furfurol-yielding material is increased. This change indicates that the pentose sugars are split off from the more complex pentosans of the apple. The enzyme producing this change was sought. Filtered extract of the mycelium, acting under aseptic conditions, is able to change xylan to xylose, but it loses its power when boiled. It is clear, therefore, that a xylanase is present in the fungus or its extract which can hydrolyze xylan.—CHARLES A. SHULL.

Plant formations of Canada.—In a brief bulletin of less than a score of pages MACOUN and MALTE[26] have outlined some of the most strikingly characteristic plant formations of Canada and noted their distribution and dominant species. It will serve to give some idea of the flora as a whole, and will indicate the wide diversity to be found, extending as it does from rich mesophytic forests of conifers and deciduous trees to xerophytic grassland and Arctic tundras.—GEO. D. FULLER.

Californian plants.—An addition to our knowledge of the vegetation of a portion of the Sierra Nevada Mountains comes in the form of an annotated list of species by PARISH[27]. The region includes associations of chaparral and conifer forests; among the latter *Pinus monophylla*, *P. ponderosa*, and *P. Murrayana* dominate at different altitudes.—GEO. D. FULLER.

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[25] HAWKINS, L. A., The utilization of certain pentoses and compounds of pentoses by *Glomerella cingulata*. Amer. Jour. Bot. **2**:375–388. 1915.

[26] MACOUN, J. M., and MALTE, M. O., The flora of Canada. Can. Geol. Survey. Museum Bull. **26**:14. 1917.

[27] PARISH, S. B., An enumeration of the Pteridophytes and Spermatophytes of the San Bernardino Mountains, California. Plant World **20**:163–178, 208–223, 245–259. 1917.

VOLUME LXV NUMBER 2

THE
BOTANICAL GAZETTE

FEBRUARY 1918

ALGAE OF THE HAWAIIAN ARCHIPELAGO. II

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The following list will indicate the specific content of the alga flora of the Hawaiian Archipelago. In so far as has been possible to obtain published records, in addition to the author's material, the list comprises practically all known Hawaiian algae. As the field has never been intensively surveyed in its entirety, there is undoubtedly a vast number of forms still undescribed. This is particularly true of the phytoplankton. The list includes brief characterizations, with special reference to habitat and geographical distribution. Items of special interest, such as economic uses, are also noted, although it has been necessary to restrict such data sharply for sake of compactness. The list is offered as a reconnaissance, and carries no implication of completeness.

The sequence of families is that of ENGLER and PRANTL; the sequence of species is that of DETONI (*Sylloge Algarum*). The determinations are principally those of TILDEN, LEMMERMANN, REED, and SETCHELL; in many cases material collected by the author has been compared with the original descriptions, and the representative stations or habitats have been confirmed, redefined, or extended. The literature concerning the habitats and ecological relations of Hawaiian algae is very scanty; the chief aim of the present paper has been that of summarizing available data, and thus indicating the need for more detailed and intensive investigations.

Schizophyceae

CHROOCOCCACEAE

Chroococcus turgidus (Kuetz.) Naegeli.—In shallow stagnant pools; collected on the slopes of Mauna Kea, Hawaii.

C. macrococcus (Kuetz.) Rabenh.—In shallow stagnant pools; collected on the slopes of Mauna Kea, Hawaii.

Gloeocapsa polydermatica Kuetz.—Plant colony gelatinous and slimy; dull green or dusky olive, often very dark; on wet cliffs and rock surfaces; from sea level up through the rain forests.

G. quarternata (Breb.) Kuetz.—Forms a gray-green or light olive mucilaginous coating on wet cliffs; abundant in the humid zones, especially near waterfalls.

G. magma (Breb.) Kuetz.—Forms a grumous, crustaceous, coppery purple mass on wet stones, in and along mountain streams, mostly between 1000 and 6000 ft.

G. thermalis Lemm.—Colonies mucous, hyaline or dark purple; characteristic of warm pools on Hawaii, especially in the Puna district.

Chondrocystis Schauinslandii Lemm.—Colony cushion shaped, widely expanded, up to 35 cm. high, cartilaginous, soft and fragile, incrusted with lime at the base; recorded only from the Laysan Island lagoon.

Gloeothece fuscolutea Naegeli.—Colonies soft, gelatinous, bright blue-green, often covering the surface of the water in the lowland rice fields and among taro patches (loi).

Aphanothece Naegeli Wartmann.—Colonies gelatinous, forming small, soft, olive-brown lumps along the margins of waterfalls, among mosses, liverworts, etc., in the rain forests and on wet cliffs.

A. prasina A. Braun.—Colonies soft, gelatinous, more or less globular; bright emerald green; forming free swimming, tuberculose, globose, or flattened masses; floating in brackish water in stagnant pools, rice patches, and similar situations.

Gomphosphaeria aponina Kuetz.—Colonies spherical, mucous, solid, and free swimming; collected among marine algae at Laysan Island.

Coleosphaeriopsis halophila Lemm.—Colonies spherical, gelatinous, hollow, known only from the lagoon of Laysan Island.

Merismopedium glaucum (Ehrenb.) Naeg.—Colonies flat, free floating, in shallow, sluggish water, such as rice fields, taro loi, etc.; sometimes very abundant, especially in late summer (Oahu).

CHAMAESIPHONACEAE

Xenococcus laysanensis Lemm.—Epiphytic, disk-shaped colonies; collected on marine algae at Laysan Island.

X. Kerneri Hansg.—Colonies irregularly expanded, crustaceous; fairly abundant in ditches and taro patches throughout the lowlands; sometimes epiphytic.

Chamaesiphon curvatus Nordst.—Epiphytic; collected among filaments of *Cladophora longiarticulata* in taro patches and ditches; not common; var. *elongatum* Nordst. is found in similar situations.

OSCILLATORIACEAE

Oscillatoria sancta Kuetz.—Colonies or plant mass dark lead colored, "becoming violet when dried and tinting the paper a beautiful violet" (TILDEN); forms a reddish brown or grayish skin on the wet sides of cliffs, waterfalls, ditches, and other moist, earthy places.

O. Bonnemaisonii Cruan.—Trichomes form loose and regular spirals; epiphytic on marine algae in Laysan Island waters; mixed with other algae, floating in lagoons within the reefs, Hawaii and other islands.

O. corallinae Gomont.—Trichomes gregarious, forming a fine, delicate coating on the surface of larger algae; collected at Laysan in washings from marine algae.

O. laetevirens Crouan.—Plant mass thin, membranaceous, bright blue-green; abundant, forming a delicate stratum covering the bottoms and sides of tidal pools in rocky places along the platform reefs; also collected among washings from marine algae at Laysan.

O. formosa Bory.—Plant mass dark blue-green; common on wet cliffs and near waterfalls, in the montane rain forests; also on the walls of wet caverns, near the mouths; these latter situations are often rich in blue-green algae.

Trichodesmium Thierbauttii Gomont.—Colonies green, forming extensive disconnected "sea blooms"; collected in plankton between Hawaii and Laysan.

T. contortum Wille.—Colonies bright yellow, spirally twisted; habit like the preceding; collected in plankton between Hawaii and Laysan.

Spirulina major Kuetz.—Plant mass dark blue-green; usually scattered among other algae, as on the sides of wet cliffs and near the mouths of the very numerous moist caverns or "lava-tubes" which honeycomb the Hawaiian mountains, from sea level to the highest summits.

S. subtilissima Kuetz.—Plant mass mucous, dark green; collected at Laysan Island in washings from marine algae.

Phormidium Crosbyanum Tilden.—Plant mass 2 cm. thick by 5 cm. diameter, impregnated with lime, somewhat hard, bluish green to reddish brown; forming flattened globose cushions on rocky shelves along the coral reefs and ledges, between tide marks.

P. papyraceum (Agardh) Gomont.—Plant mass expanded, glistening, thin, leathery, dark green; on wet rocks and cliffs, and around water-tanks, troughs, flumes, etc.; abundant.

P. laysanense Lemm.—Known only from Laysan Island, where it was collected on *Turbinaria*.

P. favosum (Bory) Gomont.—Plant mass moderately expanded, papery or thick, attached at base, floating; on sides and bottoms of irrigation ditches and troughs, tanks, etc.; not uncommon.

Lyngbya mucicola Lemm.—Epiphytic; known only from Laysan Island, where it was collected on *Chondrocystis Schauinslandii*.

L. rivulariarum Gomont.—Occurring in masses of *Nostoc*, in lowland ditches and taro patches; not uncommon.

L. subtilis W. West.—Filaments solitary and scattered; in pools and ditches in the lower zones of the larger islands.

L. distincta (Nordst.) Schmidle.—In irrigation ditches and streams; fairly plentiful; also found among the filaments of such other algae as *Pithophora* spp.

L. cladophorae Tilden.—Epiphytic on filaments of *Cladophora*, in the mountain streams.

L. Meneghiniana (Kuetz.) Gomont.—Plant mass up to 1 cm. high; caespitose, fasciculate, mucous, dull blue-green; collected on marine algae at Laysan; not known from the other islands.

L. semiplena (C. Agh.) J. Agh.—Plant mass rarely higher than 3 cm., caespitose, extensive, mucous, usually dull yellowish green or dark green; occurs in the rocky basins of tidal pools along the platform reefs of such islands as Oahu and Kauai; also collected on marine algae at the Laysan atoll.

L. confervoides C. Agh.—Plant mass 5 cm. high, caespitose, extended, fasciculate, mucous, dull yellowish or dark green; fairly common on rocky shores and in tidal pools.

L. aestuarii (Mertens) Liebman.—Plant mass widely extended, either forming a compact woolly layer on moist earth, or a floccose mass floating in water, blackish or dull blue-green; common in ditches and muddy taro patches, forming a skin over the substratum; also on sandy beaches.

forma *natans* Gomont.—Plant mass covered with water; at first attached to wet earth, later floating; filaments loosely entangled; floating in fresh water lagoons, rice fields, taro patches, etc.

forma *aeruginosa* (Agh.) Wolle.—Plant mass dark blue-green; forming conspicuous patches in shallow water of rice fields, taro patches, and similar situations.

L. majuscula (Dillwyn) Harvey.—Plant mass up to 3 cm. high or long; widely expanded; dark blue to yellowish green; filaments very long; epiphytic on other marine algae, in shallow waters along the coral reefs.

L. Martensiana Menegh.—Plant mass caespitose, blue-green; occurring on twigs, etc., under dripping water, under flumes, and tanks, and near waterfalls in the mountains; not uncommon.

L. perelegans Lemm.—Epiphytic; known only from Laysan Island, where it was collected on other marine algae.

L. Kuetzingii var. *distincta* (Nordst.) Lemm.—Occurs on the lowlands, in ditches and shallow ponds; epiphytic on such forms as *Pithophora* and *Cladophora*.

Hydrocoleus cantharidosmus (Mont.) Gomont.—Plant mass up to 2 cm. high, caespitose, slippery, olive or dark blue-green; growing with other algae in shallow waters along the coral reefs and beaches.

Inactis hawaiiensis (Lemm.) DeToni.—Filaments solitary, growing in a gelatinous mass formed by other algae; collected in warm pools on the Island of Hawaii, in company with *Gloeocapsa*, *Stigonema*, etc.

Microcoleus paludosus (Kuetz.) Gomont.—Filaments entangled, growing among other algae or forming a blackish or blue-green stratum; together with other algae it forms a layer covering rocks on the bottoms and sides of the "Green Lake" in Puna, Hawaii.

Catagnymene pelagica Lemm.—Unicellular, free floating filaments; collected in plankton between Hawaii and Laysan.

C. spiralis Lemm.—Habitat as for the preceding species; collected in plankton between Hawaii and Laysan.

Haliarachne lenticularis Lemm.—Filaments multicellular, free floating in globose or elongate colonies; collected in plankton between Hawaii and Laysan.

NOSTOCACEAE

Nostoc punctiforme (Kuetz.) Hariot.—Colonies small, globose, scattered or confluent; frequent on the wet walls of ditches and taro patches.

N. paludosum Kuetz.—Colonies very minute, scarcely visible, punctiform, gelatinous; in shallow ditches and pools.

N. Linckia (Roth) Bornet.—Colonies of various sizes, finally clathrate-fenestrate and irregularly torn, blue-green or violet; occurs with *Conferva sandwicensis* and other algae in shallow pools, taro loi, swampy places, etc., at low altitudes.

N. piscinale Kuetz.—Fairly abundant in late summer in rice fields, taro patches, irrigation ditches (au-wai), etc.

N. spongiaeforme Agardh.—Colonies at first minute, finally expanded, verrucose, bullose; in taro patches and other warm, shallow, muddy bottomed waters; fairly plentiful.

N. foliaceum Mougeot.—Colonies gelatinous, spongy, lacunose; in globules among mosses and liverworts on wet cliffs in the montane rain forest zone, and in the vicinity of waterfalls; not recorded from the lowlands.

N. commune Vaucher.—Colonies spreading out as undulating, folded, fleshy, torn or perforated sheets, leathery on the surface;

common around water troughs, tanks, flumes, and similar moist situations.

N. verrucosum (Linn.) Vaucher.—Colonies often gregarious, up to 10 cm. in diam.; at first solid, gelatinous, firm, spherical, later hollow and torn; forming small, black-green, shotlike balls, covering the sides of pools in falls and rapids of the streams in the montane rain forests; not uncommon.

Nodularia hawaiiensis Tilden.—Plant mass or colony stringy, dark green, in tufts along the outer margins of the coral reefs; constantly washed by the surf; fairly common.

Anabaena variabilis Kuetz.—Colonies gelatinous, spreading on damp soil or floating free, dark green; on bottoms and sides of irrigation ditches, taro patches, and other moist places; this, like the following species, is usually found in connection with other algal forms.

A. catenula (Kuetz.) Born. and Flah.—Colonies gelatinous, floating, blue-green; frequent in stagnant water of rice fields and taro patches; sometimes in mountain streams, but not recorded from high altitudes.

A. confervoides Reinsch.—Colonies thin; floating in taro patches and other shallow water; sometimes rather abundant, but usually rare.

Cylindrospermum stagnale (Kuetz.) Born. and Flah.—Colonies floccose, expanded, indefinite, mucous; attached or floating; on wet cliffs and in the vicinity of waterfalls, chiefly in the rain forests.

C. catenatum Ralfs.—Colonies mucous, orbicular-confluent, indefinite, blackish green; along the mountain streamways, on rocks and wet cliffs; abundant in certain localities.

Richelia intracellularis J. Schm.—Endophytic, with single trichomes; found living in the cells of *Rhizolenia styliformis* and *Hemiaulis delicatus;* collected in plankton between Hawaii and Laysan.

Aulosira Schauinslandii Lemm.—Filaments free and equal; scattered or fasciculate; collected on *Turbinaria* at Laysan.

Michrochaete vitiensis Askenasy.—Colonies loosely caespitose, short, tomentose; collected growing on *Liagora coarctata* at Laysan.

Hormothamnion solutum Born. and Grunow.—Plant mass floccose, entangled, mucous, green or blue-green; not uncommon here and there along the coral reefs, in shallow waters and in tidal pools.

SCYTONEMACEAE

Plectonema nostocarum Bornet.—Filaments graceful, elongate, at first much branched, later sparingly branched; collected in warm pools in the vicinity of Kilauea Crater, an active volcano on the island of Hawaii.

Scytonema rivulare Borzi.—Colonies widely extended, woolly, blackish, tending toward reddish or brown; forming dark brownish or purple-red cushions on stones in the mountain streams; plentiful.

S. crispum (Agh.) Bornet.—Colonies caespitose, entangled, woolly, green, becoming brown or olive; in ponds, rice fields, taro patches, and other quiet or stagnant waters on the lowlands.

S. azureum Tilden.—Cell contents deep purple-blue; with other thermophilous algae forming a layer covering rocks on the bottoms and sides of hot springs in the Puna district, Hawaii.

S. varium Kuetz.—Colonies 2–3 mm. high, cushion-shaped, bluish green or brownish; often found on wet cliffs near waterfalls, chiefly in the rain forests.

S. javanicum (Kuetz.) Bornet var. *hawaiiensis* Lemm.—Colonies cushion-shaped, dark blue-green; collected among the wet mosses, etc., in the forests near Kilauea Crater, Island of Hawaii.

S. ocellatum Lyngb.—Colonies cushion-shaped, black or gray, becoming bluish; on moist shaded rocks and wet cliffs.

S. guyanense (Montagne) Born. and Flah.—Colonies dense, cushion-shaped, 1–2 mm. thick, widely expanded, blackish green; on moist stones.

S. mirabile (Dillwyn) Born.—Colonies woolly, widely expanded, spongy tomentose, brownish black or blackish green; collected in shallow pools on the slopes of Mauna Kea, Hawaii.

S. fuliginosum Tilden.—Colonies thin, bluish green; forms thin layers on the bottoms of shallow tidal pools, along the platform reefs and rocky shores; fairly common.

Tolypothrix lanata (Desv.) Wartmann.—Colonies caespitose-floccose, blue-green, becoming brownish with age; found in shallow

stagnant pools on the slopes of Mauna Kea, adhering to leaves, etc., in the water.

T. distorta (Hofman-Bang) Kuetz.—Colonies caespitose-floccose or cushion-like, blue-green or brownish; forming tufts or cushions on stones in the mountain streams; plentiful in the montane rain forest zone.

STIGONEMACEAE

Hapalosiphon fontinalis (Agh.) Bornet.—Colonies dull blue-green, 3 mm. high; found in shallow stagnant pools on Mauna Kea, adhering to leaves and other litter.

Fischerella ambigua (Naeg.) Gomont.—Colonies crustaceous, orbicular, up to 1 mm. thick, brown becoming black; on moist soil on shady places, on the lowlands, and in the rain forests.

F. thermalis (Schabe) Gomont.—Colonies 0.5 mm. thick, cushion-shaped, woolly, expanded, blackish olive or blue-green; collected in warm pools in the vicinity of Kilauea Crater.

var. *mucosa* Lemm.—Habitat as for the species; luxuriant algal growths occur in these warm springs.

Stigonema aerugineum Tilden.—Colonies forming a brown, membranous layer on the bottoms of shallow quiet pools.

S. ocellatum (Dillwyn) Thuret.—Colonies cushion-shaped, woolly, brownish; frequent in quiet shallow pools.

S. minutum (Agh.) Hassall.—Colonies crustaceous or cushion-like, thin, fragile, blackish; collected on moist stony soil in the vicinity of Hilo, Hawaii.

RIVULARIACEAE

Calothrix confervicola (Roth) Agh.—Filaments gregarious, stellately fasciculate, attached, rigid; collected as epiphytes on marine algae, at Laysan.

C. aeruginea (Kuetz.) Thuret.—Filaments forming a somewhat continuous light blue-green layer on the surfaces of larger algae; common in tidal pools along the coral platforms and rocky shores.

C. crustacea Thuret.—Colonies caespitose, velvety, widely expanded, blackish green or brownish; epiphytic on other algae in tidal pools and along the reefs.

C. fusca (Kuetz.) Bornet and Flah.—Filaments scattered or gregarious; living within the colonies of various gelatinous algae; in ditches, taro patches, and rice fields.

C. sandvicensis (Nordst.) Schm.—Epiphytic on filaments of *Pithophora affinis*, in shallow water on the lowlands.

C. rhizoleniae Lemm.—Epiphytic on *Rhizolenia* and *Hemiaulus;* collected in plankton between Hawaii and Laysan.

Rivularia natans (Hedwig) Welwitch.—Colonies spherical, hollow, soft, dull olive-green; forming soft brown velvety masses, in rice fields and taro patches; common on the lowlands.

Chlorophyceae

SPHAERELLACEAE

Haematococcus pluvialis Flotow.—Occurs throughout the islands in shallow pools and streams, often forming reddish patches; it is a cosmopolitan species.

H. thermalis Lemm.—Abundant in the warm springs of the Puna district, Hawaii, and endemic to this region.

VOLVOCACEAE

Gonium sociale (Duj.) Warm.—Occurs in ponds, taro patches, etc., throughout the islands.

Other well known genera, such as *Volvox*, *Pandorina*, and *Eudorina*, have not been reported as yet from the islands.

TETRASPORACEAE

Dactylococcus infusionum var. *minor* Nordst.—A widely known species, frequent in streams and shallow waters.

Dictyosphaerium pulchellum Wood.—A fairly common species.

PLEUROCOCCACEAE

Gloeocystis gigas (Kuetz.) Lagerh.—Has been recorded from the swamps on the middle slopes of Mauna Kea, Hawaii.

Raphidium polymorphum Fres.—A cosmopolitan species; occurs throughout the islands in fresh waters.

Schroederia setigera Lemm.—In pools and streams.

Closteriopsis longissima Lemm.—In pools and streams.

Oocystis Naegeli A. Br.—Has been collected in swamps on the middle slopes of Mauna Kea, Hawaii.

Scenedesmus quadricauda (Turp.) Breb.—In pools and reservoirs on all the islands; var. *oahuensis* Lemm. has been collected on the lowlands of Oahu.

CHARACIACEAE

Characium ensiforme Herm.—Has been reported from the swamps on the slopes of Mauna Kea.

C. minutum A. Br.—In wet caverns and other moist habitats.

C. groenlandicum Richter.—Found growing on crustaceans in fishponds on the island of Molokai.

HALOSPHAERACEAE

Halosphaera viridis var. *gracilis* Lemm.—Collected in plankton between Hawaii and Laysan.

HYDRODICTYACEAE

Pediastrum integrum var. *Braunianum* (Grun.) Nordst.—Pools and streams.

P. Boryanum (Turp.) Menegh.—Pools and streams.

P. duplex var. *clathratum* A. Br.—Pools and streams; var. *reticulatum* Lagerh. occurs in the same habitats.

P. tetras (Ehrenb.) Ralf.—Pools and streams.

P. bidentulum var. *ornatum* Nordst.—Stagnant shallow waters.

Hydrodictyon reticulatum (L.) Lagerh.—Plentiful in rice fields, taro patches, and other shallow waters; it is called *pala-wai* by the native Hawaiians, and sometimes used by them for food. The native name is also applied to several other green fresh water algae.

OPHIOCYTIACEAE

Ophiocytium gracilipes A. Br.—A free swimming form, in shallow waters, and also in wet caves at higher levels.

CONFERVACEAE

Conferva bombycina var. *minor* Wille.—Cosmopolitan.

C. sandwicensis Agh.—Endemic; in rice fields, pools, and streams; filaments very fine and silky.

ULVACEAE

Monostroma spp.—Several unidentified species occur in brackish pools and lagoons along the reefs.

Ulva rigida Agh.—Occurs along the coral reefs of the larger islands and also the atolls.

U. fasciata Delile.—Thallus stipitate, simple or divided into acute segments; fairly common along coral reefs and beaches.

U. lactuca L. forma *genuina* Hauck.—This and var. *laciniata* (Wulf.) J. Agh. are common in shallow waters along the coasts and reefs. Frequently great quantities are thrown up on the beaches by high tides or by kona storms. *U. fasciata* is known to the natives by the names *limu paha-paha* or *limu pala-haloha*. *U. lactuca* is called *limu lipa-laha-laha* or *limu pa-ka-ea*. These grow in quiet water near the shore and are easily gathered. When air dry these species have about 18 per cent water, 14 per cent protein, 50 per cent starches, sugars, etc., and 15 per cent ash. They are commonly used as a salad food by the natives, and comprise an important element in the food of the reef inhabiting fishes.

Enteromorpha flexuosa (Wulf.) Agh.—Very common on stones, along the shores and in the harbors; cosmopolitan.

E. Hopkirkii Agh.—An obscure species.

E. intestinalis (L.) Link.—Cosmopolitan, with numerous varieties and forms; abundant in Hawaiian waters.

E. Linza (L.) J. Agh.—Cosmopolitan, with several forms; abundant in Hawaiian waters.

E. plumosa Kuetz.—Cosmopolitan; not uncommon in Hawaii.

E. prolifera (Muell.) J. Agh.—Cosmopolitan; var. *tubulosa* Kuetz. occurs in brackish pools and ditches.

E. compressa (L.) Grev.—Cosmopolitan, with numerous varieties; var. *trichodes* Kuetz. is recorded from brackish situations.

All of the Hawaiian species of *Enteromorpha* grow in shallow salt or brackish waters along the coasts, and in brackish pools and ditches. They are usually abundant at the mouths of streams, especially on the islands of Kauai and Oahu. They are easily gathered, and are all considered edible by the natives. These algae, known as *limu ele-ele*, are among the most abundant, most popular, and most widely used of the edible algae. They are com-

monly on sale in the native markets. Chemical analyses of the air dry material show about 13 per cent water, 12–19 per cent protein, 50 per cent fats and carbohydrates exclusive of crude fiber, and 10–20 per cent ash.

ULOTHRICHIACEAE

Ulothrix subtilis Kuetz. and *U. minulata* Kuetz.—These two species are common in rice fields, taro patches, ditches, and similar situations; the yellow-green, decumbent, soft, hairlike fleece is attached to the bottom or rocks; under dripping water it forms a bright green incrustation.

CHAETOPHORACEAE

Stigeoclonium falklandicum Kuetz.—Called *limu pala-wai* or *limu li-pala-wai* by the natives, and used by them for food; occurs in streams and pools; fairly abundant.

S. amoenum Kuetz.—Called *limu hulu-ilio;* grows in brackish ponds and ditches near the sea; it is eaten by only a few of the natives; a cosmopolitan species with many varieties.

S. tenue Kuetz.—One of the algae most common on the vertical cliffs of waterfalls; in these situations it frequently becomes 12–14 inches long; like the preceding, it is a cosmopolitan species with many varieties.

Draparnaldia macrocladia Nordst.—Occurs in streams and pools; fairly common in Manoa, Núuanu, Kalihi, etc.; endemic.

Aphanothece repens A. Br.—Occurs in taro patches, swamps, etc.; often epiphytic on such plants as *Cladophora;* also in most caverns, on the walls and floors, ex. Makiki Valley; a cosmopolitan species, occurring in Europe and New Zealand.

Chaetosphaeridium globosum (Nordst.) Klebahn.—Widely distributed in fresh water; thallus subglobose, of branched procumbent filaments.

OEDOGONIACEAE

Oedogonium obsoletum Wittr.—In brackish waters; also in Europe and North America.

O. globosum Nordst.—In streams; recorded only from Hawaiian Islands.

O. crispum var. *havaiense* Nordst.—In swamps and pools; a cosmopolitan species with numerous varieties.

O. Pringsheimii forma *pachydermatosporum* (Nordst.) Hirn.—Collected in the Mauna Kea swamplands; a cosmopolitan species with numerous varieties.

O. acrosporum var. *majusculum* Nordst.—Collected in the Mauna Kea swamps; another cosmopolitan species with numerous varieties.

O. longicolle Nordst.—In pools and ditches; there are several varieties in Hawaiian waters.

A number of the species of *Oedogonium* are plentiful in the mountain streams and in the vicinity of waterfalls.

Bulbochaete varians Wittr. var. *havaiensis* Nordst.—Widely distributed in temperate regions as well as in the tropics.

B. rectangularis Wittr. var. *hiloensis* Nordst.—Another widely distributed species with numerous local varieties.

COLEOCHAETACEAE

Coleochaete orbicularis Pringsh.—Thallus minute, orbicular, 2–3.5 mm. diameter; filaments numerous, articulate; cosmopolitan.

C. irregularis Pringsh.—Thallus irregular, bright green, filaments decumbent; cosmopolitan.

CLADOPHORACEAE

Chaetomorpha pacifica Kuetz.—Abundant along the shores; occurs in all tropical waters; filaments grass green, coarse and rigid.

Cladophora fracta (Dillw.) Agh.—In streams and damp caverns; a cosmopolitan species with numerous varieties.

C. inserta Dickie.—In brackish pools along the coasts.

C. Nordstedii DeT.—In pools and swamps of fresh water; rare.

C. composita Harv. and Hook.—Thallus pulvinate, spongiose, pale green; filaments delicate membranous, pellucid.

C. nitida Kuetz.—This species is called *limu hulu-ilio* (dog's hair) by the natives, and is sometimes used for food; it occurs in mountain streams and pools.

C. composita contracta Brand.—Found along the leeward shores of the island of Oahu.

C. Montagnei Waianeana Brand.—This and the preceding occur in shallow waters along the coral reefs; the species is Cuban.

C. antennina (Bory) Kuetz.—This and several other species are used locally by the natives for food, chiefly on the islands of Maui and Hawaii; they are called *limu hulu-ilio*, *limu ilio*, or *limu manu*.

BRYOPSIDACEAE

Bryopsis plumosa Kuetz.—Plentiful in quiet shallow waters, on sandy bottoms, along the coral reefs; fronds 2–6 in. long, often highly pinnatifid.

CAULERPACEAE

Caulerpa pinnata (L.) Web.—Collected at Laysan Island.

C. racemosa var. *laetevirens* Web.—Collected at Laysan; there are several varieties; the species is known from the Red Sea.

C. laxifolia (Vahl.) Agh.—Plentiful along the leeward coral reefs in shallow waters and tidal pools, resembling a miniature *Lycopodium;* occurs throughout the Pacific and Indian oceans.

CODIACEAE

Halimeda tuna (Ell. and Sol.) Lam.—Abundant in the shallow waters along the coral reefs; a cosmopolitan species, and an important member of the reef-building series of algae.

H. opuntia (L.) Lam.—Has been collected at various points along the reefs and also at Laysan; a cosmopolitan species, with many varieties and forms. The reef-building powers of *Halimeda* and its associates have undoubtedly been underestimated in the past.

Codium adhaerens (Cabr.) Agh.—Thallus crustaceous, forming a sheet on the substratum, periphery excrescent; cosmopolitan.

C. tomentosum (Huds.) Stackh.—This and the preceding are called *limu aala-ula* by the natives; plentiful in shallow reef waters; thallus cylindric, elongate, dark green; cosmopolitan.

C. Muelleri Kuetz.—Known to the natives as *limu aala-ula;* on the island of Hawaii as *limu wawae-iole* and *limu wawae-moa;* it inhabits shallow coastal waters; often on exposed rocks in the surf, or on the outer margins of the reefs. The species of *Codium* all have stout holdfasts, and require a knife or chisel to collect them.

VALONIACEAE

Valonia aegagrophila (Roth) Agh.—Thallus irregularly tubular; cosmopolitan in all warm seas.

V. confervoides Harv.—Cosmopolitan in all warm seas; common in Hawaiian waters.

V. utricularis Agh.—Called *limu li-puu-puu* by the natives, and used by them for food; these species all live along the coral reefs, and are important fish food.

Dictyosphaeria favulosa (Agh.) Dcne.—Common along the reefs and coasts in shallow waters; also collected at Laysan.

Microdictyon umbilicatum (Velley) Zanard.—Leaflike, netted thalli; fairly common in pools and shallows along the reefs; a cosmopolitan species in all warm seas.

PITHOPHORACEAE

Pithophora affinis Nordst.—Native name *limu pala-wai* or *li-pala wai;* used for food; known only from the Hawaiian Islands.

CHARACEAE

Nitella havaiensis Nordst.—In streams, brackish ditches, and pools.

Chara coronata var. *leptosperma* forma *oahuensis* (Meyen) A. Br.—In ditches and pools.

C. gymnopus var. *armata* (Meyen) Nordst.—On all the islands, in ditches, shallow pools, etc.

ZYGNEMACEAE

Mougeotia capucina (Bory) Agh.—Dark violaceous, in streams and pools; cosmopolitan, from Scotland to New Zealand.

Zygnema spontaneum Nordst.—In ditches, taro patches, rice fields, etc.; known only from the Hawaiian Islands.

Spirogyra is represented in the Hawaiian Islands by a number of species, abundant in streams and pools, both on the lowland and in the mountains; a number of them are used by the natives as food, and are called collectively *limu pala-wai.*

DESMIDIACEAE

The desmids are represented in the Hawaiian flora by the following known forms; there are undoubtedly very many forms as yet undescribed:

Desmidium aptogonium var. acutius Nordst., Gymnozyga moniliformis Ehrenb., Gonatozygon Ralfsii De Bary, Cylindrocystis Brebissonii Menegh., Closterium didymotocum var. multinucleatum Nordst., C. praelongum Breb., C. Pritchardianum Archer, C. lineatum var. sandvicense Nordst., C. dianae Ehrenb., C. parvulum Naeg., C. moniliferum (Bory) Ehrenb., C. setaceum Ehrenb., Penium lamellosum Breb., P. navicula Breb., Tetmemorus granulatus forma minor Nordst., T. levis var. continuus Nordst., Disphinctium palangula (Breb.) Hansg., D. subglobosum (Nordst.) DeToni, D. connatum (Breb.) De Bary, D. annulatum Naeg., D. speciosum var. simplex Nordst., Pleurotaenium trabecula (Ehrenb.) Naeg., P. Ehrenbergii (Ralfs) Delp., P. indicum (Gren.) Lund., P. nodulosum (Breb.) De Bary, Xanthidium armatum var. fissum Nordst., Cosmarium granatum var. subgranatum Nordst., C. Meneghini Breb., C. crenatum Ralfs, C. holmiense Lund., C. parvulum Breb. forma spetbergensis Nordst., C. sulcatum Nordst., C. depauperatum Nordst., C. anisochondrum Nordst., Arthrodesmus octocornis forma havaiensis Nordst., Euastrum binale (Turp.) Ralfs, E. ansatum Lund., E. sinuosum Lenorm., Micrasterias truncata (Corda) Breb., M. adscendens Nordst., Staurastrum subtile Nordst., S. spongiosum var. Griffithianum (Naeg.) Lagerh., S. subscabrum Nordst., S. muticum Breb., S. monticulosum var. duplex Nordst., S. margaritaceum Ehrenb., S. tenuissimum West.

This gives a total of 15 genera and 47 known species.

FLAGELLATAE

The following flagellates have been collected in ditches, taro patches, rice fields, fishponds, and other quiet, shallow waters:

Salpincoeca pyxidium S.K., Dinobryon sertularia Ehrenb., Euglena spirogyra Ehrenb., Phacus pyrum (Ehrenb.) Stein., P. pleuronectes Nitzsch., Trachelomonas volvocina Ehrenb. var. minuta Lemm., T. oblonga Lemm. var. truncata Lemm., T. hispida (Perty) Stein.

SILICOFLAGELLATAE

Several species have been taken in plankton between Hawaii and Laysan, as follows:

Dictyocha fibula var. messanensis (Haeckel) Lemm., var. stapedia (Haeckel) Lemm., Distephanus speculum (Ehrenb.) Haeckel.

PERIDINIALES

A considerable number of forms in this group have been taken in plankton between Hawaii and Laysan:

Pyrocystis fusiformis Wyv., P. pseudonoctulica Wyv., P. lunula Schuett., Hemidinium nasatum Stein., Pyrophacus horologium Stein., Ceratium candelabrum (Ehrenb.) Stein., C. furca (Ehrenb.) Clap. and Lachm., C. fusus (Ehrenb.) Duj., var. concavum Gourr., var. extensum Gourr., C. gibberum Gourr., var. contortum Gourr., C. gravidum Gourr., C. lineatum Ehrenb., C. tripos (Mueller) Nitzsch., var. arcticum (Ehrenb.) Cleve., var. arcuatum Gourr., var. horridum Cleve., var. macroceros (Ehrenb.) Clap. and Lachm., Gonyaulax polyedra Stein., G. polygramme Stein., Goniodoma armatum (Schuett.) Schmidt., Diplopsalis lenticula Bergh., Peridinium divergens Ehrenb., var. depressum (Bail.) Cleve., var. rhomboideum Lemm., P. inconspicuum Lemm., Oxytoxum Schauinslandii Lemm., Ceratocorys horrida Stein., var. longicornis Lemm., Phalacroma mitra Schuett., Amphisolenia palmata Stein., A. Schauinslandii Lemm., Histioneis quadrata (Schuett.) Lemm., H. Steinii (Schuett.) Lemm.

BACILLARIALES

The diatons are represented by a large number of forms; like the desmids, the group is very incompletely known in tropical waters.

Melosira Juergensii Agh., Gallionella nummuloides (Dill) Bory, Paralia sulcuta (Ehrenb.) Cleve., Hyalodiscus subtilis Bail., H. scoticus (Kuetz.) Grun., Sceletonema costatum (Grev.) Cleve., Cyclotella striata (Kuetz.) Grun., Coscinodiscus excentricus Ehrenb., C. dimorphus Castr., Archnoidiscus ornatus Ehrenb., Asteropampra marylandica Ehrenb., A. rotula Grev., Aulacodiscus orientalis Grev., Pyrgodiscus calyciflos. Temp. and Brun., Actinocyclus ornatus Rattr., A. Ralfsii (W.Sm.) Ralfs, A. splendens Rattr., A. Ehrenbergii Ralfs, A. subtilis (Greg.) Ralfs, Guinardia elongata Lemm., Rhizosolenia semispina Hensen., R. setigera Brightw., R. styliformis Brightw., R. temperi var. acuminata Perag., Bacteriastrum varians Lauder., Chaetoceros diversum var. tenue Cleve., C. laciniosum Schuett., C. peruvianum Brightw., Climacodium Jacobi Cleve., Triceratium arcticum Brightw., T. dubium Brightw., T. zonatula Grev., T. punctatum Brightw., T. Shadboldtianum var. robustum Lemm., Biddulphia pulchella Gray, B. reticulata Roper, B. imperialis Walker, Isthmia nervosa Kuetz., Isthmiella enervis (Ehrenb.) Cleve., Hemiaulus Hauckii Grun., H. delicatus Lemm., Terpisnoe musica Ehrenb., T. australis Ehrenb., Rhabdomena adriaticum Kuetz., R. robustum Grun., Tabellaria platystoma Ehrenb., T. rhabdostoma Ehrenb., Climacosira mirifica (W.Sm.) Grun., Striatella deliculata (Kuetz.) Grun., Grammatophora marina (Lyngb.) Kuetz., var. communis Grun., var. macilenta W.Sm., G. havaiensis Mereschk., G. angulosa Ehrenb.,

var. hamulifera (Kuetz.) Grun., Gephyria media Arnott, Opephora pacifica (Grun.) Petit., Licmomorpha flabellata (Carm.) Agh., L. remulus Grun., L. Ehrenbergii var. tenuistriata Mereschk., L. dubia Grun., L. Grunowii var. elongata Mereschk., L. Juergensii Agh., Climacosphenis moniligera Ehrenb., C. elongata Mereschk., Fragilaria capucina Desmaz., F. lamella Ehrenb., Rhaphoneis setaces Ehrenb., Synedra ulna var. splendens (Kuetz.) Brun., S. acus Kuetz., S. radians Kuetz., S. pulchella (Ralfs) Kuetz., S. affinis Kuetz., var. sandwicensis Grun., Ardissonia fulgens (Grev.) Grun., A. superba (Kuetz.) Grun., A. robusta (Ralfs) DeToni, Toxarium undulatum Bail., T. semilunare Lemm., T. Hennedyanum (Greg.) Grun., T. rostratum Hantz., Asterionella formosa Hass., A. notata. Grun., Eunotia pectinalis (Kuetz.) Rabenh., Acthnanthes glabrata (Grun.) Cleve., A. lanceolatum Breb., A. brevipes var. angustata Grev., var. pennaeformis Grev., Campyloneis Grevellei W.Sm., var. typica Cleve., Cocconeis pellucida Hantzsch., C. pseudomarginata Greg., var. intermedia Grun., C. heteroidea Hantzsch., var. sigmoides Grun., Caloneis liber var. linearis Grun., var. genuina forma tenuistriata Cleve., C. formosa Greg., Diploneis papula A.S., D. splendida Greg., D. Schmidtii Cleve., D. Weisflogii A.S., D. notabilis Grev., D. vacillans A.S., D. nitescens Greg., D. crabo var. multicostata Grun., var. minuta Cleve., Navicula cuspidata var. ambigua Ehrenb., N. pupula Kuetz., N. confervacea Kuetz., N. anceps var. obtusa Grun., N. cryptocephala Kuetz., N. rhyncocephala Kuetz., var. amphiceros Kuetz., N. consors A.S., N. cancellata var. Gregorii Ralfs, N. Zostereti Grun., N. brasiliensis Grun., N. concilians Cleve., N. Hennedyi var. tahitensis Cleve., Trachyneis aspera Ehrenb., var. pulchella W.Sm., T. antillarum var. Mereschk Cleve., T. velata A.S., Pinnularia appendiculata Agh., P. interrupta forma stauroneiformis (V.H.) Cleve., P. divergens W.Sm., P. borealis Ehrenb., P. stauroptera var. interrupta Cleve., P. acrosphaeria forma maxima Cleve., P. major Kuetz., P. viridis Nitzsch., Pleorosigma balticum (Ehrenb.) W.Sm., P. formosum W.Sm., P. rigidum W.Sm., P. angulatum W.Sm., Tropidoneis lepidoptera var. samoensis Grun., Mastogloia decussata Grun., M. fimbriata Brightw., M. minuta Grev., M. exigua Lewis, M. Goesii Cleve., M. citrus Cleve., M. pumila Grun., M. quinquecostata var. concinna A.S., M. electa A.S., Gomphonema parvulum Kuetz., G. gracile var. dichotomum W.S., G. lanceolatum Ehrenb., G. subclavatum Grun., G. olivaceum var. tenellum Kuetz., Rhiocosphenia curvata (Kuetz.) Grun., Amphora ovalis (Breb.) Kuetz., var. pediculus (Kuetz.) V.H., A. coffaeiformis Agh., A. lineolata Ehrenb., A. angusta var. eblongella Grun., Rhopalodia gibba (Ehrenb.) O.M., R. musculus (Kuetz.) O. Mueller, R. gibberula var. minuens O. Mueller, var. Vanheurckii O. Mueller, var. minuta O. Mueller, Nitzschia panduriformis Greg., var. minor Grun., N. subcostata Grun., N. Janischii Grun., N. angularis W.Sm., N. sigmoidea (Nit.) W.Sm., N. vermicularis (Kuetz.) Hant., N. sigma (Kuetz.) W.Sm., var. intercedens Grun., var. rigidula Grun., var. curvula (Ehrenb.) Grun., N. obtusa var. nana Grun., N. linearis (Agh.) W.Sm., N. palea (Kuetz.) W.Sm., N. ventricosa Kitton, N. lorenziana var. major Grun.,

N. curvirostris Cleve., var. closterium (Ehrenb.) V.H., N. acuclaris (Kuetz.) W.Sm., N. longissima (Breb.) Ralfs, N. pungens Grun., var. atlantica Cleve., Surirella fastuosa Ehrenb., S. anfractosa A.Sc., Podocystis adriatica Kuetz., Campylodiscus Grevillii Leud.-Fortm., C. kittonianus Grun.

Phaeophyceae

ECTOCARPACEAE

Ectocarpus simpliciusculus var. *vitiensis* Asken.—Along the coasts; often on other algae, for example, *Turbinaria;* also collected at Laysan.

E. indicus Sonder.—Plentiful along the coasts, in shallow waters; called *limu aka-akoa* or *limu hulu-ilio* by the natives, and in common use by them as food.

E. paradoxus Mont.—Common along the coasts and reefs.

SPHACELARIACEAE

Sphacelaria tribuloides Menegh.—Common in shallow waters along the coast.

S. furcigera Kuetz.—Fairly abundant in pools and shallow waters along the reefs.

ENCOELIACEAE

Hydroclathrus cancellatus Bory.—Abundant in shallow waters along the coral reefs; forms a stiff, olive-brown, perforated cushion, several inches in diameter.

Asperococcus bulbosus Lam.—Frequent in quiet shallows along the coast.

FUCACEAE

Turbinaria ornata J. Agh.—Abundant along the outer margins of the reefs, where it is exposed to the full force of the surf; also in deeper offshore waters; often cast up on the beaches in great quantities after storms.

T. vulgaris J. Agh.—Habitat as for the preceding, but not so abundant.

Sargassum obtusifolium J. Agh.—Known only from the Hawaiian Islands.

S. polyphyllum J. Agh. and var. *fissifolium* Grun.—Known only from these islands.

S. densum Dickie.—Known only from leeward Oahu; Honolulu Harbor.

S. incisum Dickie.—Known only from leeward Oahu; Honolulu Harbor.

S. echinocarpum J. Agh.—Recorded only from Hawaii and Fiji.

S. cymosum Agh.—Widely distributed in the Pacific and Atlantic oceans.

The species of *Sargassum* are all known as *limu kala* by the natives, and are used for food. They are probably the most abundant and widely distributed of the larger algae in the Hawaiian Islands. They grow in the shallow waters along the reefs, on stones and submerged ledges, and on the reefs themselves. In many restricted localities, for example, the leeward shores of Oahu, Kauai, and Molokai, they are more abundant than any other seaweed. The native uses have been described by REED as follows:

> *Limu kala* is sometimes broken into small pieces and soaked in fresh water until it turns dark and soft, then stuffed into salmon before it is roasted, or it is chopped with fish heads and salt. It is sometimes ripened by putting in water with a few mollusks called *leho*, salted slightly, and allowed to stand for several days before eating. *Limu kala* is more often than any other limu eaten on the beach, without any preparation other than rinsing off the sand and breaking into convenient pieces for eating with raw fish or squid. It is also sometimes put into meat gravies or stews just as it is served.

DICTYOTACEAE

Stypopodium lobatum Kuetz.—Occurs in many parts of the Pacific and Atlantic; collected at Laysan; thallus at first decumbent, later ascending; flabellate, palmatifid or lobate, concentrically zoned.

Padina Commersonii Bory.—Frequent in shallow water within the lagoons, often on muddy bottom; widely distributed in the Pacific and Atlantic oceans.

P. Pavonia (L.) Gaill.—Abundant along the coral reefs, in pools and lagoons; often growing where the water is distinctly muddy and brackish; gregarious and forming extensive colonies; occurs in many parts of the Atlantic and Pacific; called *limu pepeiao.*

Haliseris plagiogramma Mont.—Foliose parts flat, costate, dichotomous; grows far out on the outer margins of the reefs, where the heavy surf breaks, also in rather deep water. It occurs in other tropical and subtropical waters of the Atlantic and Pacific, for example, West Indies and Australia. It usually can be gathered only by diving or swimming. It grows here and there in small quantities only, on all the islands. It is a choice delicacy among the natives, who call it *limu lipoa*. It is often pounded and mixed with other seaweeds to give them its peculiar, penetrating, spicy flavor and odor. It is frequently served with meats or put into the gravy or stews to give them a peppery flavor, of which the Hawaiians are very fond. All Hawaiians like the odor and flavor of this alga, especially with raw fish. It is considered particularly delicious with raw flying fish, if simply broken and salted slightly.

H. pardalis Harv.—A very rare species, occasionally washed ashore after storms; also occurs in Australian waters; fronds linear, dichotomous.

Dictyota acutiloba J. Agh. and var. *distorta* J. Agh.—Recorded only from the Hawaiian Islands.

D. sandvicensis (Sond.) Kuetz.—Fairly abundant; also found in Australian waters, Red Sea, and Indian Ocean.

D. spinulosa Harv.—Rare; in various parts of the North Pacific.

D. dichotoma (Huds.) Lamx.—Common; widely distributed in all oceans.

The species of *Dictyota* are all called *limu alani* by the Hawaiians, but are seldom used for food, as they possess a bitter flavor.

ARTHROCLADIACEAE

Chnoospora pannosa J. Agh.—Fronds in a dense caespitose tangle, blackish, 6–10 cm. high, much branched and interwoven; reported only from the Hawaiian Islands.

C. fastigiata pacifica J. Agh.—Called by the natives *limu wawahi-wa'a* or *limu kau-pau*, and used as food; occurs in various parts of the Pacific, and also along the Atlantic shores of South America; fronds caespitose with numerous dichotomously branching fastigiate branches, color dark olive.

Rhodophyceae

BANGIACEAE

Porphyra leucosticta Thuret.—This is the famous *limu lua'u* of the Hawaiians, a very highly prized delicacy. It appears in late winter or early spring after the heavy southerly storms, and lasts for only a few days. It is found only on exposed rocks constantly dashed by the waves, so it is difficult and dangerous to collect, especially as the alga is extremely slippery and has to be scraped forcibly from the rocks in small bunches while the collector clings to his support and avoids the heavy waves. REED states as follows:

> He must be sure-footed, quick, and a good swimmer, if he collect *limu luau*. . . . . It is prepared by washing in the usual way in fresh water. It is then salted a little and put into clear water, where it becomes slippery and colors the water a lovely violet color. Sometimes *opihi*, a kind of limpet, is put in with the limu and salt in water, and placed in bottles or jars. This is used as needed, for it keeps many weeks when placed in the weak brine with the limpets.

Limu luau is considered a great delicacy in the few localities where it occurs, but it lasts so short a season, is so scarce, and so difficult to get that it is not very widely known. Only on northern Kauai, northern Maui, and northern Hawaii is it in use or in great favor, as it does not occur in other places, except a few scattered plants on Oahu and Molokai.

HELMINTHOCLADIACEAE

Liagora valida Harv.—Collected at Laysan; also occurs in the Atlantic and around Madagascar; often calcareous.

L. coarctata Zanard.—Collected at Laysan.

L. decussata Mont.—Called *limu pu-aki* by the natives, and considered edible; grows along the coral reefs in quiet shallow water, often in mud or sand or on small stones; fronds filiform, virgate-ramified, calcareous.

CHAETANGIACEAE

Galaxaura lapidescens (Soland) Lamx.—Fronds cylindric or compressed, subtubular, incrusted with lime; along the coral reefs in shallow waters; a common species in warm seas.

G. spongiosa Kuetz.—Habitat same as the preceding.

Scinaia furcellata (Turn.) Biv. and var. *undulata* (Mont.) J. Agh.—Fronds solitary or clustered, arising from a disklike base, several times dichotomous; cosmopolitan, with several varieties.

Actinotrichia rigida (Lamx.) Descne.—Widely distributed in the Pacific and Indian oceans, and in the Red Sea.

GELIDIACEAE

Gelidium attenuatum (*?*).—Name used by REED; not listed by DETONI; probably a synonym.

G. corneum (*?*).—Name used by REED; not listed by DETONI; probably a synonym.

G. felicinum Bory.—Occurs in the Pacific Ocean.

G. intricatum (Agh.) Kuetz.—Listed as occurring in Hawaiian waters; according to DETONI an obscure species.

G. latifolium Born.—Cosmopolitan; abundant in Atlantic and Adriatic; common in Hawaiian waters.

G. cartilagineum (L.) Gaill.—In the Pacific and Atlantic oceans.

G. pusillum (Stackh.) Le Jol.—A cosmopolitan species.

The species of *Gelidium* are all called *limu loloa*, sometimes *limu ekaha-kaha*, by the natives, and are extensively used for food. They grow on exposed black lava rocks, near the tide line, in rough water, where they are constantly washed by the surf. They have tenacious holdfasts, and require a knife or chisel for collecting. These algae are abundant along the rocky shores of Kauai, Oahu, and Molokai, and also occur in considerable quantities on the other islands. They produce a dark, viscid gelatine, strongly flavored, but suitable for glue manufacture. REED states that "our species of *Gelidium* are undoubtedly as gelatinous as the Japanese species, but they are not nearly so plentiful."

Wrangelia penicillata Agh.—This beautiful, delicate, olive green, fernlike species inhabits tidal pools along the reefs and rocky shores; cosmopolitan.

Pterocladia capillacea (Gmel.) Bornet.—Uncommon; used by the natives of Kauai and Maui, and known by them as *limu loloa;* occurs also in Mediterranean and Atlantic.

GIGARTINACEAE

Gigartina papillata (Agh.) J. Agh.—Frond flat, simple or apparently dichotomous, segments truncate-cuneate; recorded only from the Hawaiian Islands and the Golden Gate.

Gymnogongrus vermicularis americana J. Agh.—A cosmopolitan species.

G. disciplinaris (Bory) J. Agh.—Recorded from various parts of the Pacific.

These algae are generally called *limu ua-ua-loli* by the natives, but there are also a number of other native names: *limu ekaha-kaha*, *limu ko-ele-ele*, *limu awiki-wiki*, *limu nei*. They grow far out on the coral reefs, along the outer margin, where the surf is heavy. All have tough, strong holdfasts. They are most abundant on Maui and Molokai, and are rather scarce in Hawaii.

Abnfeltia concinna J. Agh.—Native name *limu aki-aki* or *limu eleau*. A succulent, brittle, reddish brown alga, abundant on partially submerged lava rocks along the coasts. It shows a preference for exposed black lava rocks, in rough water, where it receives the heavy surf. It occurs in large quantities in these habitats along the shores of Kauai, Oahu, and Hawaii, and is plentiful here and there in a few localities on the other islands. Sometimes it grows in quiet coves or behind lava ledges in less exposed places. This seaweed is relished by the natives and is commonly sold in the markets. Its air dry composition is, roughly, water 20 per cent, protein 5 per cent, starches, sugar, etc., 55 per cent, crude fiber 3 per cent, ash 15 per cent. In the fineness and clarity of its gelatine this alga is exceeded only by *Gracilaria coronopifolia*.

A. Durvillaei (Bory) J. Agh.—Recorded from various parts of the Pacific.

RHODOPHYLLIDACEAE

Eucheuma nudum J. Agh.—Frond terete, subcompressed, dichotomously branched; recorded only from the North Pacific.

SPHAEROCOCCACEAE

Sphaerococcus coronopifolius (Good. and Wood.) Agh.—Fronds dichotomously branched; fairly common; also occurs in many parts of the Pacific and Atlantic.

Gracilaria coronopifolia J. Agh.—This species is called *limu manauea*, and is extensively used for food by the Hawaiians. It grows in shallow water along the reefs, on sandy bottoms, and in stormy weather often drifts ashore in considerable quantities. It is plentiful along the low beaches of leeward Kauai, Oahu, and Molokai. Because of the less favorable coasts, it is not abundant on Maui, and less so on Hawaii. The season of greatest abundance is spring and early summer, although it is fairly plentiful throughout the year. It is one of the limus commonly offered for sale in the native fishmarkets. Its air dry composition is, roughly, water 12 per cent, protein 8 per cent, starches, sugars, etc., 58 per cent, crude fiber 3 per cent, and ash 17 per cent. It makes fine clear gelatine of excellent quality, and requires less cooking for its preparation than do the other algae.

G. confervoides (L.) Bory.—Widely distributed in all oceans; fronds long, terete, much branched; edible, but not common.

Hypnea nidifica. J. Agh.—Intricately caespitose, expanded; known from various parts of the Pacific Ocean.

H. armata (Mert.) J. Agh.—Elongate; corymbosely branched. This and the preceding species are known as *limu huna* and are among the most commonly eaten of the Hawaiian seaweeds. They are especially relished by the natives when boiled with octopus. They are abundant along the coral reefs, in shallow waters, and often drift ashore in considerable quantities. The species of *Hypnea* are common on Kauai, Oahu, and Molokai; scarce on Maui, and very rare on Hawaii. They are outranked by both *Gracilaria* and *Ahnfeltia* in the quality and quantity of their gelatine.

RHODOMENIACEAE

Plocamium sandvicense J. Agh.—Known only from the Hawaiian Islands, leeward shores of Oahu; fronds pinnately decompound, very beautiful.

Champia compressa Harv.—Fronds branched, tubular, nodose, purple, gelatinous, membranous; known to the Hawaiians as *limu o-olu;* common along the reefs, both in shallow water and farther out. Its distribution is very irregular. Also in the South Pacific and African waters.

Chylocladia rigens (Agh.) J. Agh.—Edible, called *limu akuila* or *limu kihe;* common in many parts of the Pacific.

DELESSERIACEAE

Martensia flabelliformis Harv.—Plentiful in shallow waters along the reefs; fronds flat, dichotomous, with eccentric subimbriate lobes; also recorded from Samoa.

BONNEMAISONIACEAE

Asparagopsis Sanfordiana Harv.—A very delicate plant, resembling a miniature pink conifer. It grows far out along the margins of the reefs, in the shallow waters where the surf breaks. It has a number of Hawaiian names, *limu kohu* being the most common. On Maui, Molokai, and Kauai it is often called *limu lipa-akai* or *limu lipehu.* REED states that it is always pounded well as it is being cleaned, to free it from adhering bits of coral, and also that the subsequent soaking may the more thoroughly remove the disagreeable bitter flavor. It is soaked 24 hours or more in fresh water, to remove the bitter iodine flavor. It is then salted ready to be served as a relish or salad with meats, fish, or poi, or it is mixed with other seaweeds and put into hot gravy and meat stews. *Limu kohu* has a pleasant, although slightly bitter, flavor. It is sold in the form of balls about the size of a large baseball; the price is usually 25 cents per ball; it is always in great demand. At Moloaa, on the island of Kauai, a crude kind of culture of *limu kohu* is carried on. The natives have cleared out all of the other seaweed from the reef, so that the *Asparagopsis* does not suffer from competition, and is here much finer and more luxuriant than at any other place.

RHODOMELACEAE

Laurencia nidifica J. Agh.—Reported only from the Hawaiian Islands.

L. papillosa (Forst.) Grev.—Abundant; widely distributed in all seas.

L. obtusa (Huds.) Lamx.—Frequent; a cosmopolitan species.

L. vaga Kuetz.—According to DETONI probably a form of *perforata.*

L. pinnatifida (Gmel.) Lam. and var. *osmunda* Lam.—Reported.

L. perforata Mont.—Frequent; also in the tropical Atlantic.

L. virgata (Agh.) J. Agh.—Rare; in Pacific and African waters.

The species of *Laurencia* are known to the Hawaiians by various names; *limu maneo-neo* for the shorter, coarser species, *limu li-pee-pee* for the finer, longer forms. *Limu lipee* is a contracted phrase; *limu li-puu-puu*, a name used locally in certain districts on Maui and Hawaii. The species of *Laurencia* grow in shallow waters along the reefs, either on sandy bottom, or in rocky places. They are frequently washed ashore in considerable quantities by high tides or stormy weather. The natives use all the species for food, and the prepared *limu* may be purchased in the fishmarkets.

Chondria tenuissima var. *intermedia* Grun.—Called *limu o-olu* by the natives, who use it for food; abundant on the broad, shallow, sandy bottomed inshore waters of Kauai, Oahu, and Molokai; easily gathered. It prefers quiet water and rarely grows in places exposed to the surf. Common in the fishmarkets.

Polysiphonia tongatensis Harv.—According to DeToni probably a synonym for *P. mollis*.

P. polyphysa Kuetz.—According to DeToni probably a synonym for *P. ferulacea*.

P. ferulacea Suhr.—Common; widely distributed in all oceans.

P. mollis Hook. and Harv.—Called *limu pu-alu* or *limu hawane* by the natives; it is not popular, and is seldom used as food.

Amansia glomerata Agh.—The beautiful dark red rosettes of this alga are common in deep shady pools and crevices in the coral reef; Hawaiian names are *limu li-pepe-iao* or *limu pepe-iao*, and the natives use it for food.

CERAMIACEAE

Griffithsia ovalis Harv. (?).—A very rare species; sometimes used for food on Maui and southern Hawaii; called *limu moo-puna*, *limu ka-lipoa*, and *limu au-pupu*.

Ceramium clavulatum Agh.—Known by a number of native names; *limu hulu-ilio*, *limu hulu*, and *limu hulu wawae-iole;* abundant in shallow waters, within the reefs, growing on sandy bottoms, and easily gathered.

C. Kuetzingianum Grun.—Fronds minute, thin, branched; epiphytic on other seaweeds; also occurs in the South Pacific.

GRATELOUPIACEAE

Halymenia formosa Harv.—Rare; native name *limu lepeahina;* fronds gelatinous, flat, stipitate, much branched; also occurs in the South Pacific.

Grateloupia filicina (Wulf.) Agh.—Abundant in shallow waters within the reef; on sandy bottom and on rocks. Known to the Hawaiians as *limu paka-ele-awa'a* or *limu hulu-hulu-waena;* the former name is used exclusively on Kauai, the latter on Hawaii; both names are used on the intermediate islands. This alga also occurs in many other seas.

SQUAMARIACEAE

Peyssonnelia rubra Descne.—In shallow waters along the reefs, in company with such algae as *Halimeda Opuntia;* adherent to the substratum; sometimes calcareous; in many other seas.

CORALLINACEAE

Mastophora tenuis Descne.—Reported only from the Hawaiian Islands.

Amphiroa fragilissima (L.) Lamx.—Collected at Laysan; also abundant in the Indian Ocean, and along the shores of Peru.

Corallina sandvicensis Reinbold.—Collected at Laysan; fronds 4–5 cm. high; known only from Laysan.

The coralline algae have not been worked up taxonomically; there are probably 15 or 20 species in addition to the preceding.

COLLEGE OF HAWAII
HONOLULU

CHEMICAL BASIS OF CORRELATION[1]

I. PRODUCTION OF EQUAL MASSES OF SHOOTS BY EQUAL MASSES OF SISTER LEAVES IN BRYOPHYLLUM CALYCINUM

JACQUES LOEB

(WITH EIGHTEEN FIGURES)

In this paper the term correlation will signify the inhibiting influence which the growing buds of a leaf of *Bryophyllum calycinum* have upon the growth of other buds of the same leaf. It is generally known that in a complex organism the growth in one organ of the complex may inhibit the growth in other organs of the same complex.

In former papers[2] the writer has shown that when in *Bryophyllum calycinum* one organ inhibits the growth of buds in another organ the inhibited organ contributes in some cases material to the growth in the inhibiting organ. It was known through the experiments of WAKKER and DEVRIES[3] that if a piece of stem is left attached to a leaf of *Bryophyllum* the stem will inhibit the growth of shoots in the notches of the leaf, while such shoots will grow if the leaf is entirely isolated from the stem. The writer was able to show that in such a case the leaf accelerates the growth of a shoot in the stem attached to the leaf. Thus figs. 1 and 2 are sister leaves, that is, leaves from the same node of a stem of *Bryophyllum*. Both are dipping with their tips in water.[4] Leaf 1, without a stem, has formed a shoot in 22 days, while the sister leaf in fig. 2 has formed no shoot, due to the inhibiting effect of the piece of stem attached to the leaf. The latter has accelerated the growth of the shoot in the piece of stem attached to the leaf, however, for a piece of stem of

[1] From the Laboratories of The Rockefeller Institute for Medical Research.

[2] LOEB, J., BOT. GAZ. **60**:249. 1915; **62**:293. 1916; Science **41**:704. 1915; The organism as a whole, p. 153. Putnam's Sons, New York. 1916.

[3] DEVRIES, H., Jahrb. Wiss. Bot. **22**:35. 1890–91.

[4] The result is the same when the leaves are suspended in moist air instead of dipping into water.

equal size without a leaf attached to it will in the same time form no shoot or only a very tiny shoot (fig. 3). The inference was drawn that the inhibiting effect of the stem upon the leaf in fig. 2 was due to the fact that the leaf furnished the material required for the growth of shoots to the stem instead of to its own notches. This takes place even when no shoot is formed in the stem; in that case the material furnished by the leaf is stored in or consumed by

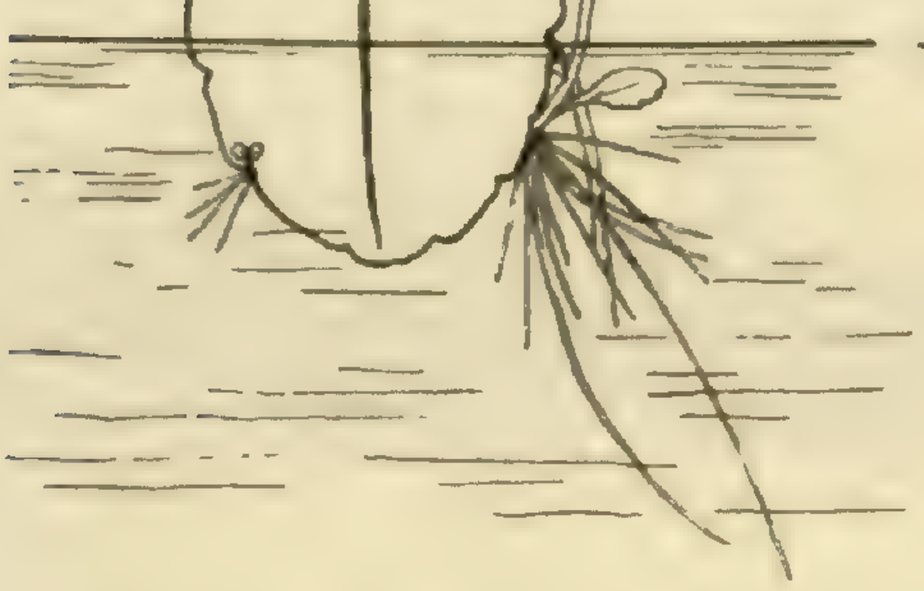

FIG. 1

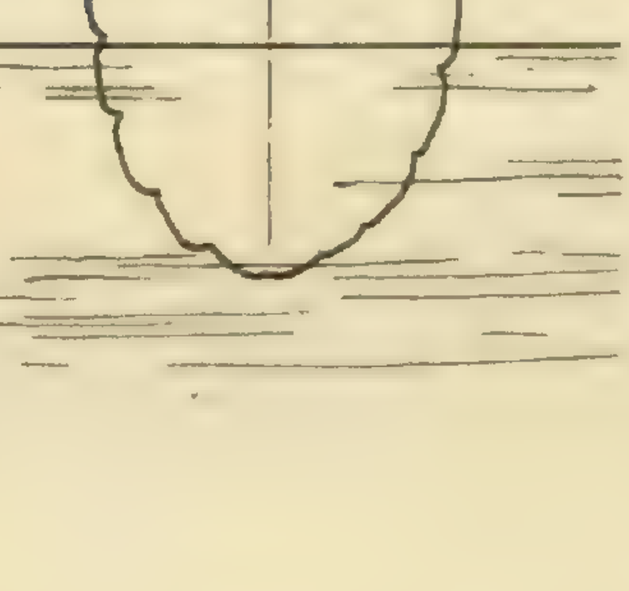

FIG. 2

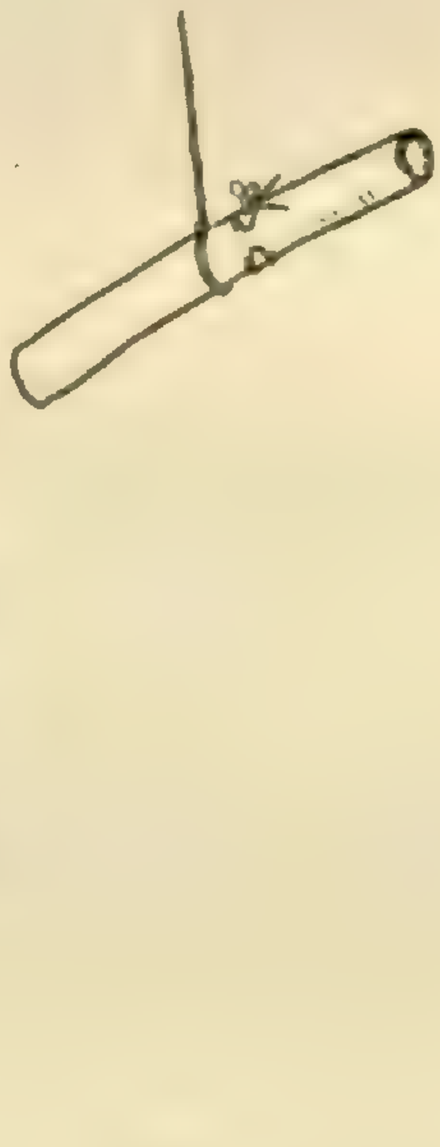

FIG. 3

FIGS. 1–3.—Figs. 1, 2, sister leaves; leaf of fig. 2 still attached to stem, showing stem inhibits shoot formation in leaf; fig. 2 shows inhibition is accompanied by accelerating effect of leaf upon growth of shoot from stem, since in a piece of stem, suspended in moist air, as in fig. 3, production of shoots is suppressed or retarded.

certain cells of the stem, as indicated, for example, by callus formation and by geotropic curvature.[5]

The same principle was shown to hold if stems without leaves are suspended in moist air. In such cases the two buds of the most apical node of a long piece of stem grow out (fig. 4), and it can be shown that the basal part of the stem whose buds are inhibited from growing furnishes to the growing buds at the apex

[5] LOEB, J., Science 46:547. 1917.

the material required for their growth, for if we cut out short pieces with one node only (fig. 4, *a*, *b*, *c*, *d*), the growth of the shoots from the buds is retarded. This is not the only factor of inhibition in this case, since the writer has recently shown[6] that a growing bud, as well as a leaf, seems to send out inhibitory substances toward the base of the stem which prevent the buds in the stem, situated more basally, from growing out. This factor of inhibition will not be considered in this paper.

We shall try to show in this paper that the quantity of material available for the formation of shoots is definite and limited, and that inhibition may result from the retention or utilization of part of this material by the inhibiting organ. A preliminary note of these results has already been published.[7]

Each notch of a leaf of *Bryophyllum calycinum* can give rise to a shoot when the leaf is cut off from the stem and suspended in moist air, but as a rule only a few of these notches will grow into new plants. When we cut the leaf into as many pieces as there are notches, practically each piece (very small ones only excepted) will give rise to a shoot. Figs. 5 and 6 are sister leaves. Leaf 5 is cut into as many pieces as there are notches, while leaf 6 is left intact. Both were kept on moist filter paper. Leaf 5 has given rise to a new shoot in practically each notch, while leaf 6 has formed only 4 shoots. We assume that in the latter leaf the shoots which

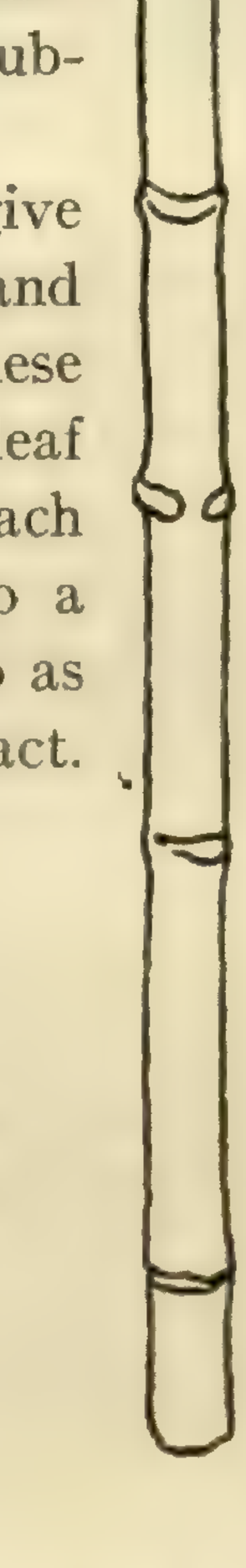

FIG. 4.—Shows that inhibited basal part of the long stem accelerates growth of the two apical buds, since in pieces with one node only (*a*, *b*, *c*, *d*) the buds do not grow at all, or much more slowly.

[6] LOEB, J., Science **46**:547. 1917. [7] *Ibid.*, **45**:436. 1917.

grow out first inhibit the growth in the other notches. (No part of the leaf of *Bryophyllum calycinum* except the notches is able to give rise to shoots or roots. The formation of roots will be omitted from consideration in this paper in order to simplify the discussion.) Our contention is that this inhibition in leaf 6 is due to the absorption of all the material available for shoot formation by the 4 notches that happened to grow out first, thus depriving the other notches of the material needed for the growth of shoots. By comparing figs. 5 and 6 it will be noticed that 3 of the shoots which leaf 6 produced are considerably larger than the individual shoots

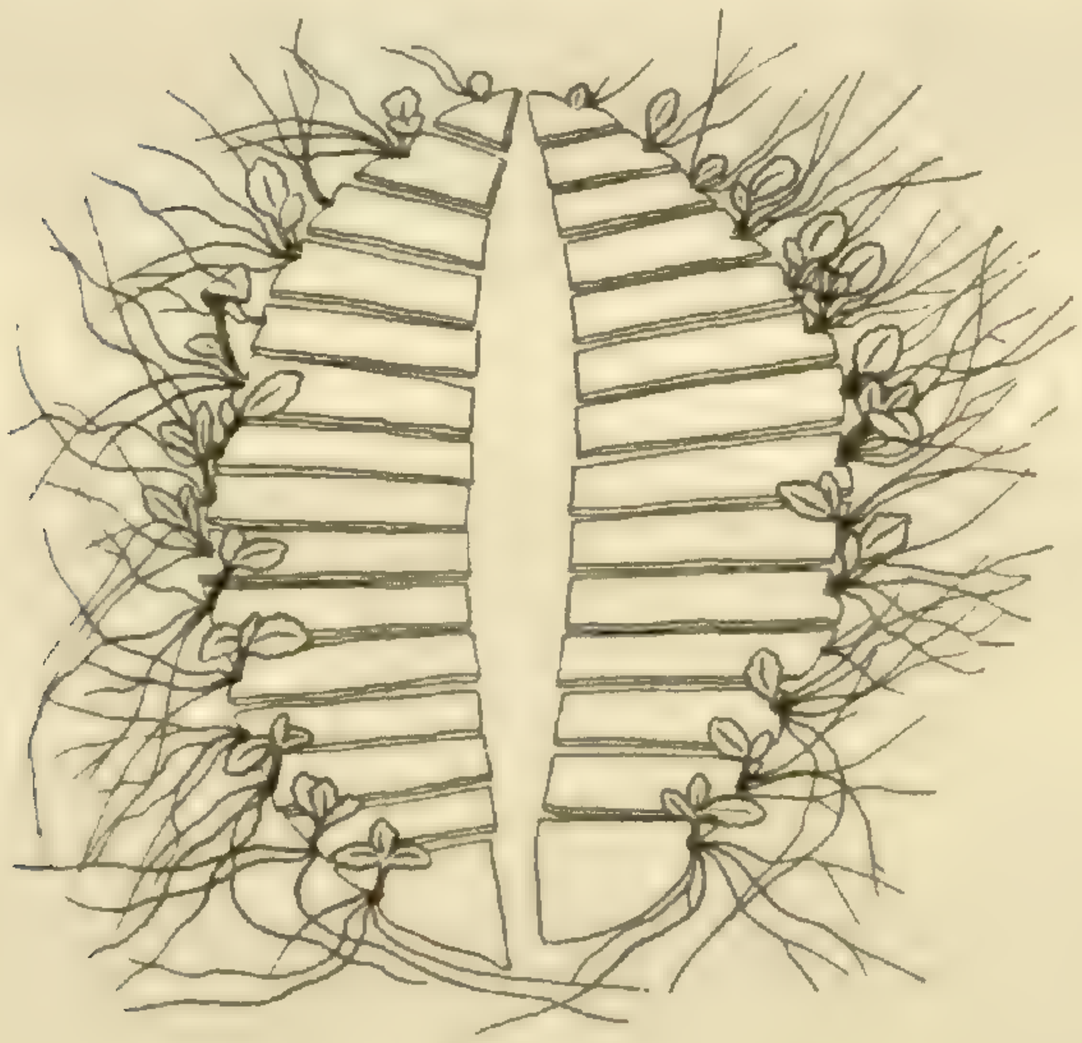

FIG. 5

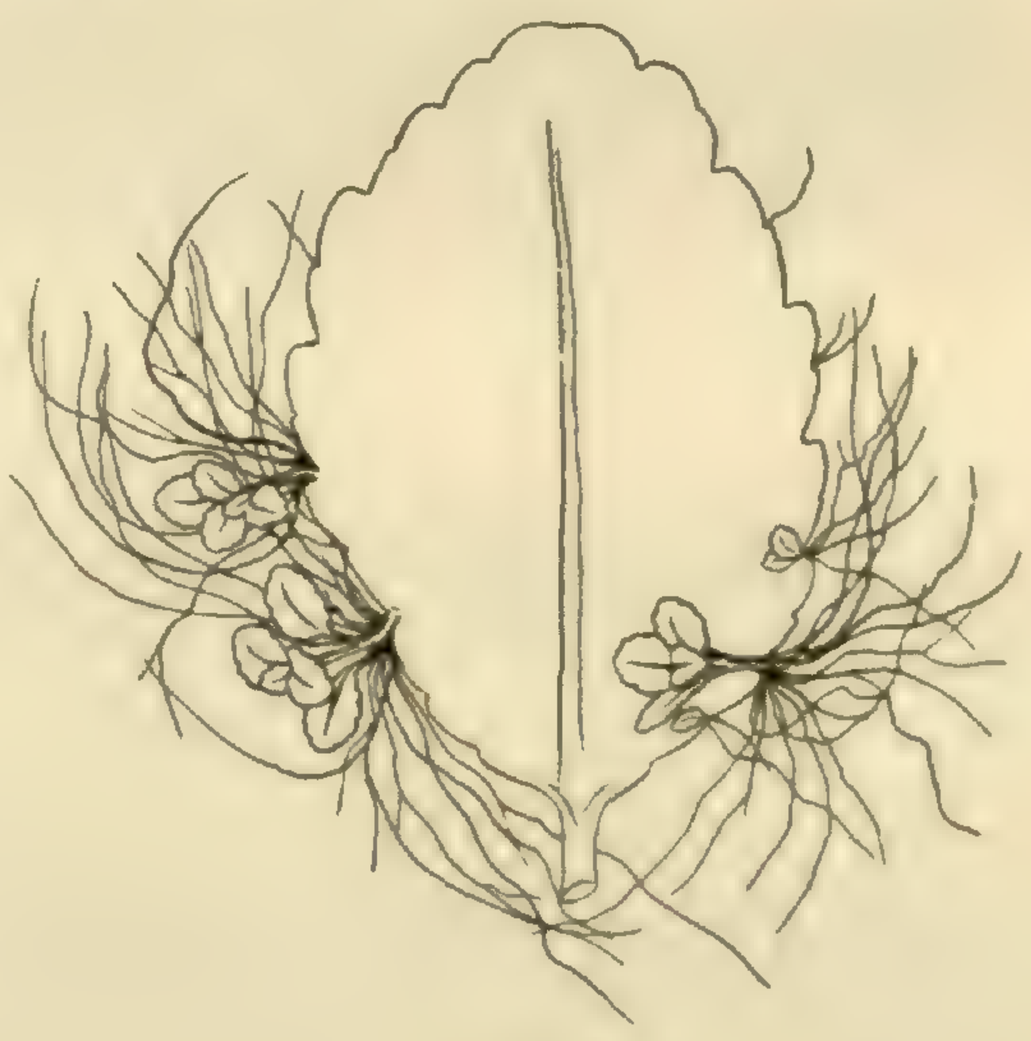

FIG. 6

FIGS. 5, 6.—Sister leaves: fig. 5, leaf cut into as many pieces as notches; almost every notch forms a shoot; fig. 6, leaf intact, only 4 shoots formed, 3 being considerably larger than those shown in fig. 5, thus indicating tendency of both leaves to produce equal masses of shoots, although number of shoots may vary considerably.

of leaf 5, and this suggests the possibility that the isolation of a piece with one notch simply prevents the material needed for the growth of the notch being taken away by some of the other notches which by chance start growing a little earlier.

In order to prove this we must be able to show that if we isolate two sister leaves (which are of equal size, age, and history) and keep them under equal conditions, they will produce in equal times approximately equal masses of shoots. It is necessary, of course, that both leaves are healthy and not yet beginning to etiolize, and that they should not do so during the course of the experiment.

It is necessary also that the experiment be continued long enough (that is, a month or longer at about 23°C.) to allow the shoots to reach a sufficiently large size, since if the shoots are too small the error in measuring their masses prevents exact results. On the other hand, the experiment must not last too long, for if the shoots become too large they produce themselves too considerable a share of the material needed for their own growth. The leaves were generally kept on wet filter paper in flat dishes with a loose glass cover. One of the greatest sources of error or variation in the results was probably the differences in the absorption of water by the roots of different leaves or pieces of leaves. Furthermore, light is an important factor in determining the masses of shoots produced, and when leaves are suspended in an aquarium and able to shade each other, inequality of illumination of sister leaves also forms a source of error. The new shoots can be cut off from the leaf comparatively neatly, although slight variations or errors are unavoidable in this operation. The shoots were freed from water droplets on their surface and weighed fresh, on the assumption that the dry weight under the conditions of the experiment is a fairly constant fraction of the fresh weight, which has been found to be approximately correct. The leaves were usually but not always weighed without their petioles.

TABLE I

Sister leaves		Number of shoots produced from leaf	Mgm. of shoots produced in 33 days
I.	Leaf 1.....	3	350
	Leaf 2.....	3	345
II.	Leaf 1.....	1	290
	Leaf 2.....	2	306
III.	Leaf 1.....	2	375
	Leaf 2.....	4	385
IV.	Leaf 1.....	5	594
	Leaf 2.....	4	607
V.	Leaf 1.....	4	457
	Leaf 2.....	5	455

Table I gives the weight of the shoots produced by 5 pairs of sister leaves in 33 days (February 15—March 20). The two sister

leaves are always designated as 1 and 2. It is found that each of two sister leaves which were of equal size produced almost identical masses of shoots in the same period of time and under equal conditions, although the number of shoots by two sister leaves differed.

Table II gives another experiment of the same kind. The two sister leaves produce in each case almost identical masses of shoots

TABLE II

MARCH 29—APRIL 20, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I.	Leaf 1	7	0.2560	2.3030	111
	Leaf 2	9	0.2455	2.2555	109
II.	Leaf 1	5	0.1920	1.783	108
	Leaf 2	4	0.2075	1.8735	111
III.	Leaf 1	5	0.2005	2.262	89
	Leaf 2	3	0.1605	1.982	81
IV.	Leaf 1	5	0.1910	1.668	114
	Leaf 2	4	0.1570	1.402	112
V.	Leaf 1	4	0.3205	2.5125	128
	Leaf 2	7	0.3760	3.0770	122
VI.*	Leaf 1	3	0.1790	2.191	82 etiolized
	Leaf 2	?	0.0595	1.597	37 leaves
VII.	Leaf 1	6	0.2355	2.6495	89
	Leaf 2	4	0.216	2.288	94
VIII.	Leaf 1	2	0.109	1.326	82
	Leaf 2	4	0.132	1.505	88
IX.	Leaf 1	3	0.172	1.927	89
	Leaf 2	5	0.187	2.093	89
Average	Leaves 1	.....	1.675	16.430	102
	Leaves 2	.....	1.682	16.476	102

* Pair VI is not included in the average.

in the same time, although the number of shoots varies quite often. The shoots produced by the two leaves of the sixth pair differ considerably, but those two leaves were etiolized. They were excluded from the calculation of the average shoot production, which is exactly the same for each set of leaves, namely 102 mgm. of shoots for 1 gm. of leaf.

Tables III and IV show a slightly greater variation than tables I and II, owing to the inevitable errors in such experiments (errors in cutting off and ascertaining the weight of the small shoots, errors in evaporation, differences in the condition of the two sister leaves,

TABLE III

APRIL 11—MAY 10, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I.	Leaf 1	2	0.180	1.655	109
	Leaf 2	1	0.201	1.590	126
II.	Leaf 1	2	0.115	1.050	109
	Leaf 2	2	0.166	1.505	110
III.	Leaf 1	3	0.155	1.081	143
	Leaf 2	2	0.140	1.098	127
IV.	Leaf 1	3	0.123	1.158	106
	Leaf 2	3	0.126	1.245	101
V.	Leaf 1	2	0.110	1.038	106
	Leaf 2	2	0.089	0.995	90
VI.	Leaf 1	2	0.183	1.646	111
	Leaf 2	2	0.153	1.383	111
VII.	Leaf 1	3	0.231	1.617	143
	Leaf 2	3	0.178	1.463	122
VIII.	Leaf 1	4	0.220	1.547	142
	Leaf 2	2	0.146	1.172	125
IX.	Leaf 1	3	0.119	1.230	97
	Leaf 2	3	0.149	1.410	106
Average	Leaves 1	.....	1.436	12.022	119
	Leaves 2	.....	1.348	11.861	114

and in the external conditions of moisture and light, and others). The fact that these errors are accidental is proved by the proximity of the average shoot production in each set of leaves, which is 119 and 114 mgm. of shoots per gm. of leaf in table III, and 106 and 100 mgm. in table IV.

We may make the following statement, therefore: *Two healthy, isolated sister leaves of equal mass will produce in equal times and under equal conditions approximately equal masses of shoots, although*

the number of shoots in the two leaves may differ. The variations in the results lie within the limits of the unavoidable errors of the experiments.

TABLE IV

INTACT SISTER LEAVES; MARCH 20—APRIL 18, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf in 29 days
I.	Leaf 1	3	0.127	1.310	97
	Leaf 2	2	0.128	1.170	109
II.	Leaf 1	2	0.150	1.595	94
	Leaf 2	3	0.1325	1.323	100
III.	Leaf 1	4	0.2085	1.9175	109
	Leaf 2	2	0.1575	1.722	91
IV.	Leaf 1	3	0.270	2.286	118
	Leaf 2	4	0.145	1.586	91
V.	Leaf 1	2	0.147	1.3385	110
	Leaf 2	5	0.2075	2.061	101
VI.	Leaf 1	4	0.211	1.9735	107
	Leaf 2	3	0.220	2.0275	107.5
VII.	Leaf 1	2	0.1065	0.9435	113
	Leaf 2	3	0.105	1.062	99
VIII.	Leaf 1	5	0.233	2.332	100
	Leaf 2	4	0.228	2.2595	101
Average	Leaves 1	.....	1.452	13.69	106
	Leaves 2	.....	1.322	13.21	100

It would follow that if we cut a leaf into two symmetrical halves each half should produce equal masses of shoots in the same time and under the same conditions. This is approximately correct, as table VI shows.

The experiment was repeated (table V), and we may confine ourselves to a statement of the average result. The two halves are designated as right and left, when facing the observer with their basal end and when lying on their lower side.

It is obvious, therefore, that if leaves are cut symmetrically, the two halves will produce in equal times and under equal conditions on the average exactly the same mass of shoots, even when the number of shoots in the two halves varies.

While in the preceding experiments the number of shoots produced in sister leaves was not identical, yet it seemed of interest to find out whether the law of the production of equal masses of shoots by equal masses of sister leaves was true also if the number

TABLE V

APRIL 12—MAY 15

	Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
20 left halves of leaves.....	33	2.916	19.307	151
20 right halves of leaves....	31	2.790	18.466	151

TABLE VI

SISTER LEAVES, EACH CUT INTO TWO SYMMETRICAL HALVES; APRIL 3—MAY 4

Sister leaves			Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I.	Leaf 1	Left half....	2	0.188	0.936	203
		Right half...	2	0.183	0.959	191
	Leaf 2	Left half....	1	0.202	1.009	200
		Right half...	2	0.254	1.241	205
II.	Leaf 1	Left half....	1	0.057	0.427	133
		Right half...	2	0.053	0.398	133
	Leaf 2	Left half....	1	0.063	0.441	143
		Right half...	1	0.056	0.398	141
III.	Leaf 1	Left half....	1	0.120	0.820	146
		Right half...	3	0.111	0.758	146
	Leaf 2	Left half....	1	0.116	0.713	163
		Right half...	1	0.115	0.721	160
IV.	Leaf 1	Left half....	1	0.070	0.497	141
		Right half...	1	0.072	0.580	124
	Leaf 2	Left half....	2	0.073	0.595	122
		Right half...	1	0.068	0.522	130

of shoots produced in the two leaves differed considerably. For this purpose one leaf was cut into 4 pieces while its sister leaf remained intact. The whole leaves produced fewer shoots than the leaves cut into 4 pieces; nevertheless, the masses of shoots produced in the two sets of leaves remained the same. Thus 12

intact leaves produced 25 shoots, while their sister leaves cut into 4 pieces each produced 50 shoots. Yet the average weight of shoots produced per gm. of leaf was 156 mgm. for the intact leaves and

TABLE VII

SISTER LEAVES, ONE INTACT, THE OTHER CUT INTO FOUR PIECES; APRIL 18—MAY 18, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I.	Leaf 1, intact.....	2	0.198	1.170	169
	Leaf 2, 4 pieces....	4	0.2025	1.205	168
II.	Leaf 1, intact.....	2	0.216	1.596	135
	Leaf 2, 4 pieces....	4	0.214	1.560	137
III.	Leaf 1, intact.....	1	0.305	1.925	158
	Leaf 2, 4 pieces....	4	0.368	2.110	174
IV.	Leaf 1, intact.....	2	0.340	1.9015	177
	Leaf 2, 4 pieces....	4	0.2635	1.475	179
V.	Leaf 1, intact.....	2	0.197	1.072	184
	Leaf 2, 4 pieces....	4	0.200	1.227	163
VI.	Leaf 1, intact.....	3	0.265	1.743	152
	Leaf 2, 4 pieces....	6	0.292	1.675	174
VII.	Leaf 1, intact.....	2	0.2415	1.741	138
	Leaf 2, 4 pieces....	4	0.255	1.745	146
VIII.	Leaf 1, intact.....	1	0.195	1.260	155
	Leaf 2, 4 pieces....	4	0.109	0.660	165
IX.	Leaf 1, intact.....	2	0.218	1.198	182
	Leaf 2, 4 pieces....	4	0.209	1.110	188
X.	Leaf 1, intact.....	2	0.223	1.514	147
	Leaf 2, 4 pieces....	4	0.180	1.280	140
XI.	Leaf 1, intact.....	4	0.258	1.820	142
	Leaf 2, 4 pieces....	5	0.2615	1.818	144
XII.	Leaf 1, intact.....	2	0.227	1.498	151
	Leaf 2, 4 pieces....	3	0.191	1.205	158
Average	Intact leaves	25	2.884	18.435	156
	Leaves cut into 4 pieces	50	2.747	17.070	161

161 mgm. for the leaves cut into 4 pieces, in spite of the difference in the number of shoots produced. Table VII gives the results in detail. These experiments again confirm the conclusion that equal

masses of sister leaves produce equal masses of shoots in equal time, even if the number of shoots in the two cases is in the ratio of 1:2.

In order to test further this law it seemed necessary to modify the experiment. For this purpose the mass of one of two sister leaves was reduced by cutting out a large piece from the center, leaving the edge intact (fig. 8), while the other leaf remained intact (fig. 7). If the law just expressed is correct, it should follow

FIG. 7

FIG. 8

FIGS. 7, 8.—Sister leaves suspended in moist air: fig. 7, leaf intact; fig. 8, leaf with mass reduced by cutting out large piece from center of leaf; mass of shoots produced smaller than that produced by intact leaf; drawn 23 days after beginning of experiment.

that the mass of shoots produced by such sister leaves (one set of which remained intact while the mass of the other set was reduced by cutting out pieces from the middle) would no longer be equal, but would differ in proportion to the mass of the two sets of leaves. This was found to be approximately true, as table VIII indicates.

Thus in experiment I (table VIII) the 5 intact leaves weighing 13.8 gm. produced in 37 days 1405 mgm. of shoots, while their 5

sister leaves, whose weight was reduced from approximately 13.8 gm. to 7.6 gm. (by cutting out pieces from the center of the leaf as indicated in fig. 8), produced in the same time and under the same condition 755 mgm. of shoots. While the proportion of the mass of the two sets of leaves was $\frac{7.6}{13.8}$, the proportion of the mass

TABLE VIII

Number of experiment	Sister leaves	Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I. Leaves dipping in water; duration of experiment 37 days	(*a*) 5 leaves, with center cut out ..	11	0.755	7.61	99
	(*b*) 5 sister leaves, intact.....	9	1.405	13.80	101
II. Leaves dipping in water; duration of experiment 25 days	(*a*) 7 leaves, with center cut out...	21	1.213	9.899	122
	(*b*) 7 sister leaves, intact.....	25	1.995	16.935	118
III. Leaves dipping in water; duration of experiment 32 days	(*a*) 9 leaves, with center cut out ..	22	2.292	10.522	218
	(*b*) 9 sister leaves, intact.....	30	3.430	17.852	192
IV. Leaves dipping in water; duration of experiment 27 days	(*a*) 12 leaves, with center cut out ..	33	2.175	11.245	194
	(*b*) 12 sister leaves, intact.....	33	2.761	19.395	142
V. Leaves kept in moist air; duration of experiment 38 days	(*a*) 5 leaves, with center cut out ..	13	0.690	5.42	109
	(*b*) 5 sister leaves, intact.....	20	1.207	11.81	102

of the shoots produced was $\frac{755}{1405}$. These two quotients are almost identical. The same is true for experiments II, III, and V, while in IV there is a greater discrepancy. Experiments III and IV indicate that if there is such a discrepancy it seems to be in favor of the leaf reduced in size. Since light plays such an important rôle in the production of shoots the discrepancy may possibly be due to the accidental fact that the intact leaves shaded

each other more in these experiments than the leaves with their centers cut out.

FIG. 9.—Sister leaves: one cut into 4 pieces, other not subdivided, but all notches except one removed; from this notch a shoot is produced considerably larger than each of shoots produced from the 4 smaller pieces of other leaf; photographed 19 days after beginning of experiment.

The shoots produced by the whole leaves and by the leaves reduced in mass, therefore, were approximately in proportion with the masses of the two sets of leaves; or in other words, each set of sister leaves produced

approximately the same weight of shoots per gram of leaf in the same length of time.

When a leaf is isolated and put on moist filter paper or if it is suspended in moist air, as a rule more than one notch grows out into a shoot (fig. 6). This seems to indicate that the material available for shoot formation in one leaf does not all flow easily into one notch, so that we should expect that the material available in a leaf might be utilized more completely if the leaf were cut into several smaller pieces than if all the material had to go into one shoot only. This fact is evident from the following experiment.

In one leaf the whole edge (containing the notches) with the exception of one notch was removed (fig. 9). Such a leaf could form only one shoot. The sister leaf was cut into 4 pieces but the edges were left intact. These 4 pieces could form at least 4 shoots. Fig. 9 shows such a pair of sister leaves. It was to be expected that the total weight of the shoots formed by the 4 pieces would be approximately equal to that of the one shoot in the sister leaf, or exceed it slightly for the reason indicated. Table IX shows that 6 shoots produced in 6 whole leaves differed very little in weight from the 32 shoots produced by their 6 sister leaves, each of which was cut into 4 pieces, but that the difference was in favor of the leaves cut into 4 pieces. The latter produced per gram leaf 93 mgm. of shoots, the former 84 mgm. In a second set of experiments the difference was in the same direction, but a little larger, namely 98 mgm. and 74.5 mgm. (table IX). While these experiments confirm the law of equal production of shoots by equal masses of leaf, they also indicate that several shoots can consume the material available in one leaf more quickly than if only one shoot is present.

A second complication is encountered when small pieces containing one notch are cut out from a leaf (fig. 6). In this case it may happen that when the piece is too small the notch of the small piece may not form any shoot at all, or the growth may be materially delayed. This is intelligible on the assumption that if the quantity of material available falls below a certain minimum no shoot can grow out. Fig. 10 illustrates this statement. A large and a small piece were cut out from the same leaf, each piece containing one notch only, the notches in each set of two pieces originally being

symmetrical. The photograph was taken 36 days after the beginning of the experiment. It will be seen that the size of the shoot varies with the size of the piece, but that some of the smallest pieces have failed to form shoots. This fact is to be considered in experiments in which one leaf is left intact and the sister leaf cut into as many pieces as there are notches. In that case it may happen that the law of equal production of shoots by equal masses of leaves

TABLE IX

SISTER LEAVES: (*a*) WHOLE LEAF, BUT ALL NOTCHES WITH EXCEPTION OF ONE REMOVED; (*b*) CUT INTO 4 PIECES, BUT NO NOTCH REMOVED; APRIL 5—APRIL 25, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots per 1 gm. of leaf
I.	(*a*) Whole leaf.....	1	0.1935	2.403	81
	(*b*) 4 pieces.....	6	0.206	2.267	91
II.	(*a*) Whole leaf.....	1	0.110	2.234	49
	(*b*) 4 pieces.....	6	0.105	2.431	43
III.	(*a*) Whole leaf.....	1	0.136	1.647	83
	(*b*) 4 pieces.....	5	0.185	2.083	89
IV.	(*a*) Whole leaf.....	1	0.196	1.8325	107
	(*b*) 4 pieces.....	7	0.2975	2.387	125
V.	(*a*) Whole leaf.....	1	0.201	2.035	99
	(*b*) 4 pieces.....	4	0.246	2.225	110
VI.	(*a*) Whole leaf.....	1	0.110	1.086	101
	(*b*) 4 pieces.....	4	0.154	1.4015	109
		Total number of shoots	Total weight of shoots	Total weight of leaves	Shoots per gm. of leaf; mgm.
Average	(*a*) Whole leaves.	6	0.9465	11.237	84
	(*b*) Cut leaves...	32	1.193	12.794	93

may not hold strictly, for two reasons: (1) some of the small pieces may not form any shoot at all or form it only too late; (2) a complication may vitiate the result in the opposite direction, namely, that the shoots formed by small pieces can use the material available for shoot formation more readily than the shoots in the whole leaves. Table XI gives the results of such an experiment on 3 pairs of sister leaves, one leaf remaining intact or cut into two symmetrical halves, while the other was cut into as many pieces as there were notches.

In spite of the enormous difference in the number of shoots in both cases, the weight of shoots produced by one gram leaf in a given time was not very different, the average being 143 mgm. of shoots in one set and 150 mgm. in the other set per gram of leaf.

The law of equal production of shoots by equal masses of leaves explains why the shoots growing out from the notches of a leaf grow the more rapidly the smaller their number. It does not explain

TABLE X

SISTER LEAVES: (*a*) WHOLE LEAF, BUT ALL NOTCHES WITH EXCEPTION OF ONE REMOVED; (*b*) CUT INTO 4 PIECES, BUT NO NOTCH REMOVED; APRIL 4—APRIL 25, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots per 1 gm. of leaf
I.	(*a*) Whole leaf.....	1	0.201	2.202	90.5
	(*b*) 4 pieces.....	6	0.316	2.542	124
II.	(*a*) Whole leaf.....	1	0.144	2.0325	71
	(*b*) 4 pieces.....	4	0.2335	2.3235	100.5
III.	(*a*) Whole leaf.....	1	0.162	1.832	88
	(*b*) 4 pieces.....	4	0.179	1.950	92
IV.	(*a*) Whole leaf.....	1	0.147	2.152	68
	(*b*) 4 pieces.....	4	0.256	2.5145	102
V.	(*a*) Whole leaf.....	1	0.150	2.710	55
	(*b*) 4 pieces.....	4	0.191	2.667	72
VI.	(*a*) Whole leaf.....	1	0.084	0.986	85
	(*b*) 4 pieces.....	4	0.111	1.107	100
		Total number of shoots	Total weight of shoots	Total weight of leaves	Shoots per gm. of leaf; mgm.
Average	(*a*) Whole leaves.	6	0.8889	11.915	74.5
	(*b*) Cut leaves ...	26	1.2875	13.104	98

how it happens that in an isolated leaf not all the notches grow out into shoots.

When we cut off a leaf and suspend it in moist air (the air not being completely saturated with water vapor), after some time most of the notches form roots, as the leaf in fig. 11 indicates, which was drawn 18 days after the beginning of the experiment. If there are any notches which do not form roots, they are usually found at the apex and at the base of the leaf (fig. 11). After the roots are

formed, shoots begin to grow out of the notches, and now a remarkable change occurs. Fig. 12 shows the same leaf as fig. 11, 10 days

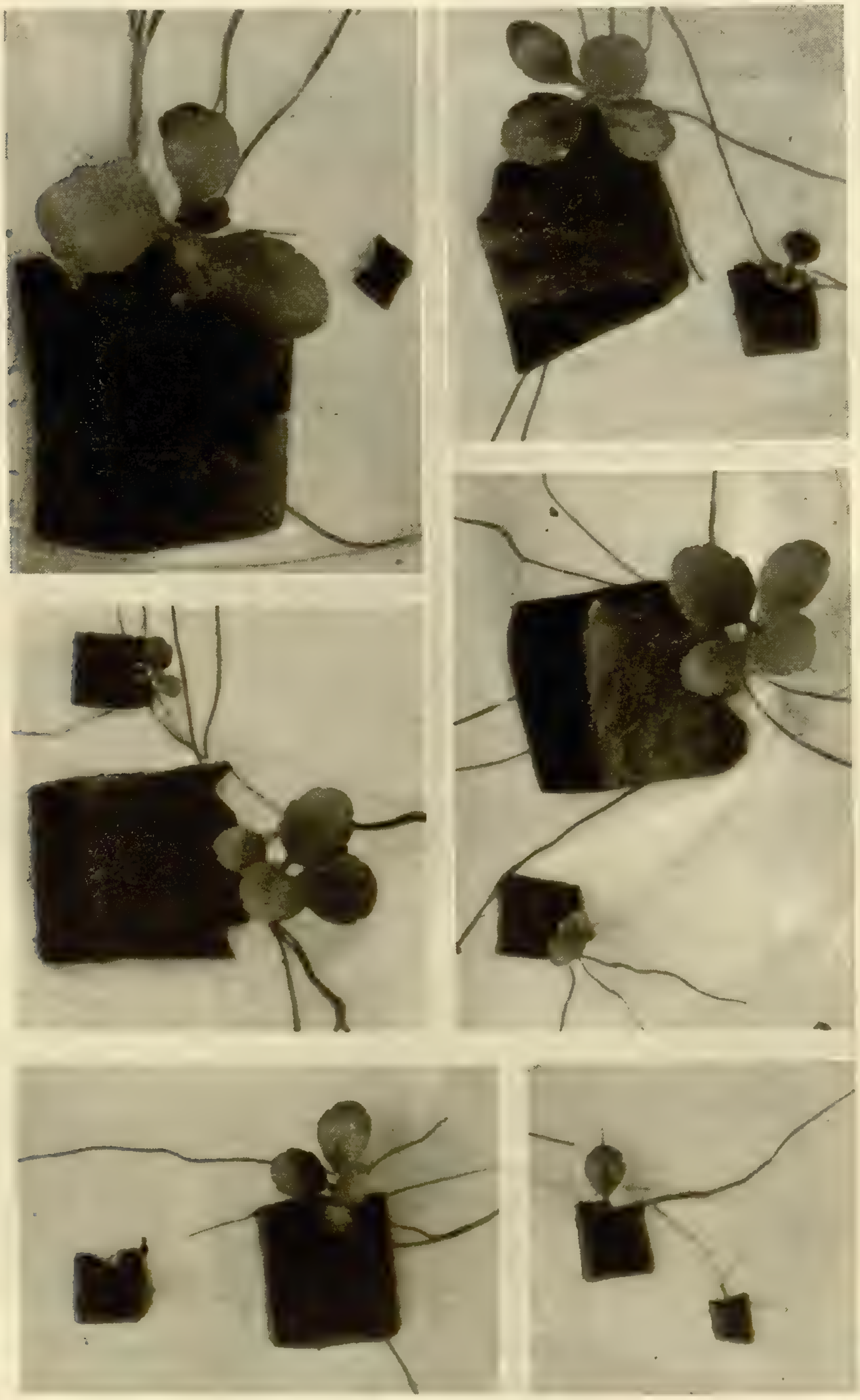

FIG. 10.—Large and very small pieces, each with one notch cut from one leaf; smallest pieces have not yet formed shoots (in 4 weeks); parallelism between size of leaf and size of shoot obvious.

later. Two of the shoots in the notches in the middle of the leaf have grown into shoots, and in these notches the roots have continued to grow; while the roots formed in the other notches have shriveled up and no new shoots have grown out.

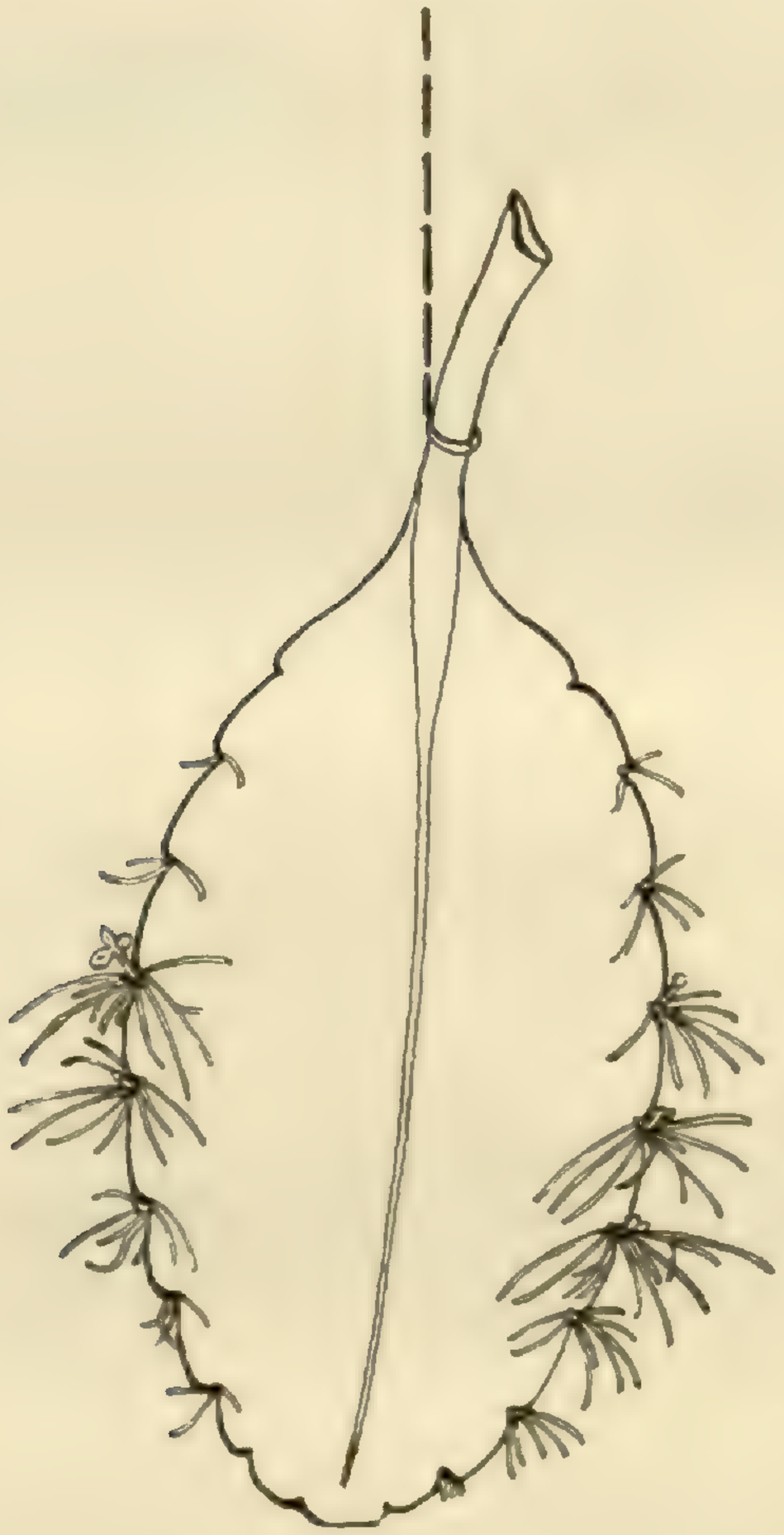

FIG. 11

FIG. 12

FIGS. 11, 12.—Same leaf suspended in moist air, in fig. 11 after 18 days, in fig. 12 after 28 days; at first all notches in middle of leaf form roots and in some of them shoots begin to develop (fig. 11); later (fig. 12) only two of these shoots in middle of leaf grow, while roots in other notches not only ceased to grow but are shriveled up; proves inhibiting effect of most rapidly growing notches on others.

From this observation, which is typical and which has been verified many times, we are inclined to draw the following conclusion. As long as the leaf is part of the normal plant, its sap flows into the stem of the plant and the notches cannot grow out. When the leaf is separated from the plant and suspended in moist air, this flow ceases and the material carried in the form of sap

remains in the leaf and becomes available for the notches. As a consequence the notches in the leaf begin to grow out. The chances for growth are apparently not equal for all the notches of a leaf suspended in moist air, but are as a rule better for those in the middle of the leaf, where the leaf is thicker and where probably more sap is available. The roots grow out before the shoots begin

TABLE XI

FEBRUARY 15—MARCH 20, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots per gm. of leaf
I.	(a) 2 halves	3	0.316	1.866	170
	(b) 16 pieces	14	0.345	1.727	200
II.	(a) Whole leaf	4	0.490	2.061	233
	(b) 14 pieces	14	0.312	1.810	172
III.	(a) Whole leaf	2	0.450	4.465	100
	(b) 17 pieces	15	0.300	3.17	95
Averages	Whole or half leaves	9	1.256	8.392	150
	Leaves cut into small pieces	43	0.957	6.71	143

to grow. Those shoots which happen to grow out first now become a center of attraction for all the material available for growth in the leaf, and they thereby inhibit not only the growth in most of the other notches but actually cause the roots formed in other notches to dry out again, as a comparison of fig. 12 with fig. 11 shows. We cannot yet tell how it happens that the more rapidly growing leaf attracts the sap to itself.

We have mentioned that as a rule the notches which will grow out first are not the ones at the apical or basal ends, but in the middle of the leaf, where the leaf is thickest and where apparently more sap is available. That it is possibly only the quantity of water which decides the initiation of growth[8] is suggested by the fact that a leaf, like the one in fig. 12, which, when suspended in moist air forms no shoots in the apical notches, can be caused at

[8] This refers only to the initial step of starting the growth in a dormant bud; its actual growth, of course, depends upon the supply of sugar, amino acids, salts, and other solutes from the leaf.

any time to form new shoots in these notches if we let the apex dip into water. As soon as this happens these notches will form shoots and these shoots will soon equal or exceed in size the old stems, and in turn may now inhibit the growth of the latter.

The leaf in fig. 12 was drawn on January 30. On February 7 its apex was suspended in water and soon new shoots formed in the apical notches (figs. 13, 14). Fig. 13 was drawn 9 days, and fig. 14,

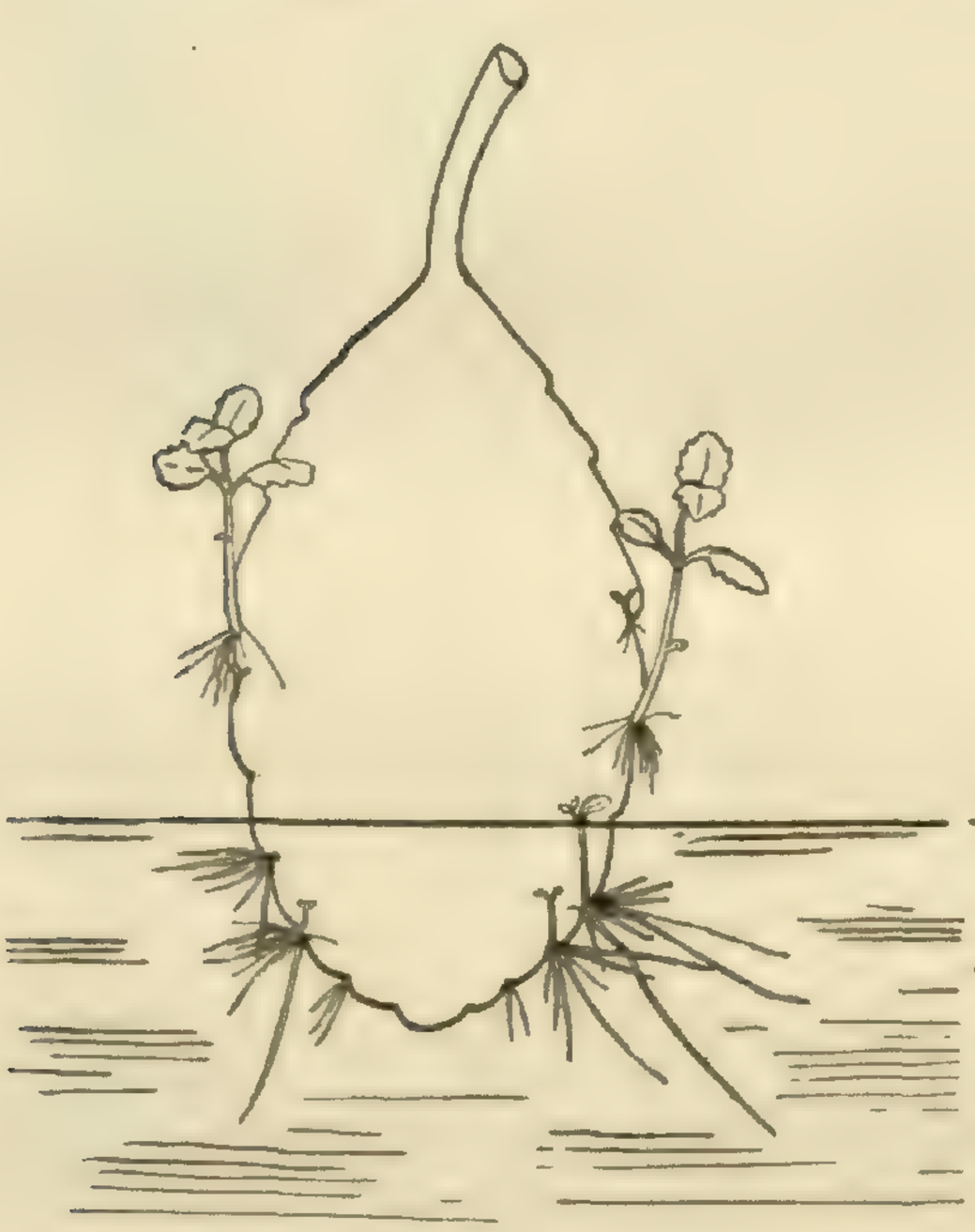

FIG. 13

FIG. 14

FIGS. 13, 14.—Same leaf as in figs. 11 and 12, after 45 and 52 days; on 33d day leaf was dipped with apex in water and now new shoots are formed in watered notches, which grow rapidly and soon reach size of two original shoots; proves that amount of water determines which notches shall grow into shoots.

16 days after the apex was put into water. It will be noticed that new shoots have grown out from three of the apical notches dipping in water. This never happened when the leaves remained in moist air. It can be shown that such a leaf when dipping in water absorbs water, and we are justified therefore in assuming that the increase in the contents of water in a notch or the starting of a current of water through the notch starts its growth.

We may compare the conditions for the initiation of the growth of a notch in a leaf to those of the growth of a seed, inasmuch as in both cases an absorption of water is necessary to initiate growth.

In both cases the water may play the rôle of accelerating the velocity of certain chemical processes which are needed for the formation of roots and shoots.

The experiment just described never fails, and we may therefore say with some justification that *in an isolated leaf suspended in moist air those notches will grow out first which by chance have at first the necessary supply of water* (*or of sap in general*). Those shoots which grow out first will then automatically inhibit the growth of the other notches by drawing the solutes and the water toward themselves.

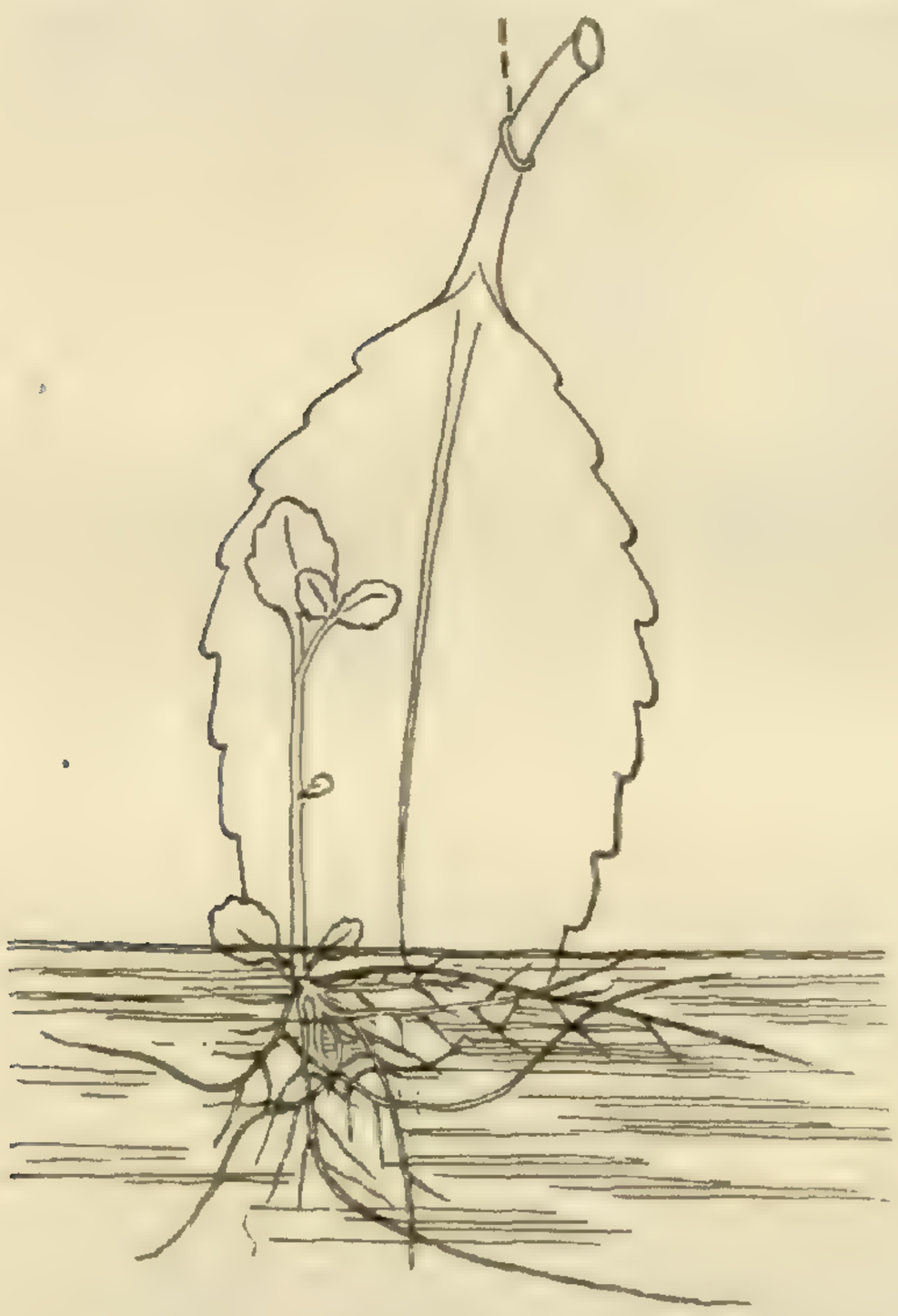

FIG. 15.—Leaf dipped with apex in water; drawn after 28 days: in such cases the shoot from one of watered notches will grow out so rapidly that as a rule it suppresses root and shoot formation in notches in middle of leaf, where growth is most rapid, when leaf is suspended in moist air, as comparison of figs. 15 and 11 will show.

This view is supported by another set of experiments. In the previous experiment the isolated leaves were first suspended in moist air and afterward allowed to dip into water. When we let the apex of the isolated leaf dip from the beginning into water, only those notches will give rise to shoots which are just under the level of the water or just above it (fig. 15). Such shoots grow more rapidly than the shoots of leaves suspended entirely in moist air, and this fact also suggests that it is the quantity of water which decides which notches grow out first. It is also noticeable that when an isolated leaf dips into water from the beginning the notches in the middle of the leaf, which would have given rise to roots (fig. 11) if the leaf had been suspended entirely in air, now generally fail to do so (fig. 15), if the leaf is not too large, presumably because the greater rate of growth of the notch dipping into water inhibits the growth of roots in the rest of the notches. With the greater

rate of growth of a notch is linked a greater inhibiting power upon the growth of the other notches, inasmuch as the flow of sap is directed toward a rapidly growing notch. The leaf in fig. 15 was then taken out of water and suspended in air on February 4. No new notches grew out, as was to be expected. The rapidly growing original shoot attracted all the sap available. A few roots started in some of the notches, but shriveled up almost as soon as they were formed (fig. 16). The results of this experiment are as constant as those of the previously mentioned experiment.

FIG. 16.—Same leaf as fig. 15: on 33d day leaf was removed from water and suspended in moist air; rapidly growing old shoot prevents any further growth in other notches.

These observations thus give us a rather clear view of the mechanism of correlation in an isolated leaf. In order to start the growth of a notch it is necessary that a stream of water should reach the notch. This will not happen as long as the leaf is part of a stem. Only when the leaf is old, ready to drop from the plant, do we notice occasionally that a shoot may form in the notches of a leaf while it is still attached to the plant, but this is rare. We can start the growth of notches at will, however, when the leaf is cut off. In that case that notch or those notches will grow first which happen to receive the greatest water supply (from within or without). Those which begin to grow more rapidly than the rest will automatically cause a current of sap toward themselves, in a way not yet understood.

They thereby inhibit or retard the growth in the other notches. This inhibition can be overcome at any time by supplying more water to an inhibited notch from without, whereby we accelerate the rate of chemical reactions in this notch, which in turn will now cause a flow of sap toward itself, but we can also increase the flow of sap to certain notches from within. The writer's former observations have shown that the sap in the leaf can flow around a corner, a fact which suggests the existence of

many interlocking channels for the sap flow. It occurred to us that if we suspend such leaves in moist air with their longitudinal axes put horizontally (figs. 17, 18), the notches on the lower side of the leaf should form more shoots than the notches on the upper side, since the sap should collect in larger masses on the lower edge of the leaf. This is apparently the case, since very often shoots form only on the lower side of such a leaf, as in fig. 17 (where the notches in *a*, *b*, *c* had been removed before the experiment began). In fig. 18 three notches formed on the lower and one on the upper side. The

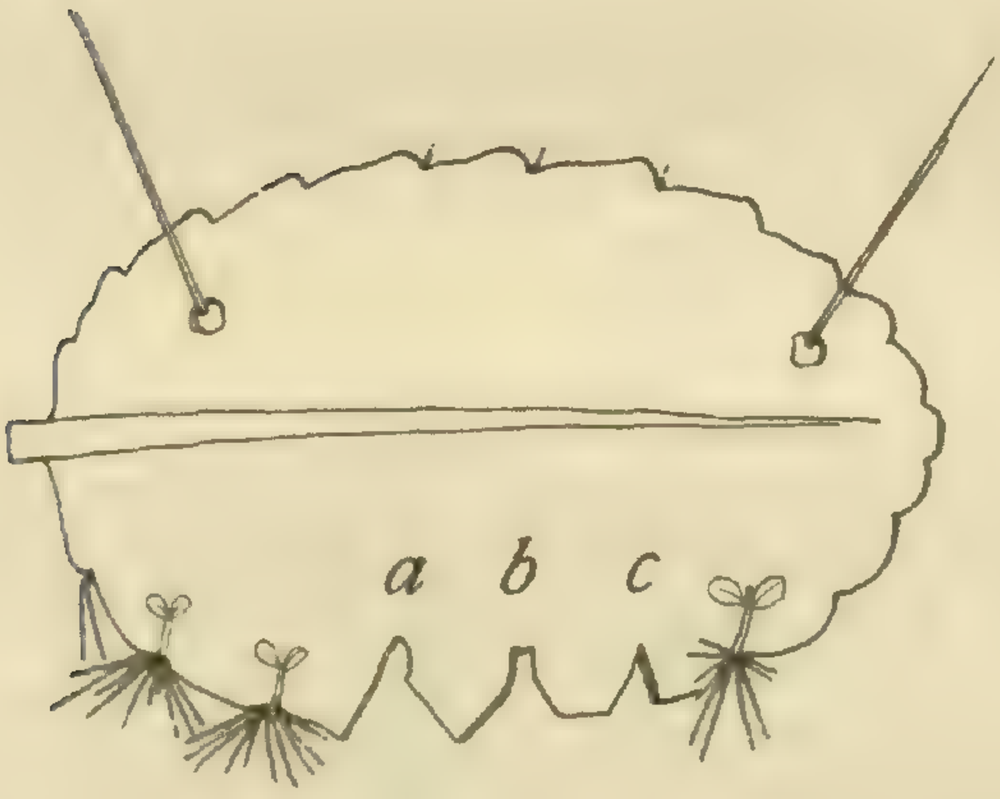

FIG. 17

FIG. 18

FIGS. 17, 18.—Leaves suspended in moist air with main axis in horizontal position: shows formation of shoots is favored on lower side, where water is bound to collect in larger masses; in fig. 17 notches at *a*, *b*, *c* had been removed.

experiment just mentioned and which has often been repeated supports the idea that the first shoots grow out where the water or sap collects, the water naturally having the tendency to flow downward.

Light is an important factor in the shoot production of the leaf of *Bryophyllum calycinum*. Isolated leaves kept in the dark produce a considerably smaller mass of shoots than their sister leaves kept in light, as the following experiment shows. Six leaves taken from different plants or nodes were suspended in the dark, either in moist air or were dipped with their apices in water; while their sister leaves were suspended in the same way but in light. Table XII shows the difference in the amount of shoot production.

It is obvious that in both cases the shoot formation is considerably greater in the light than in the dark. The experiment seems to indicate that either the process of assimilation contributes directly or indirectly to the formation of material for shoots in the leaf, or that the light in some other way contributes to the shoot formation. It is obvious that among the conditions which are to be considered in the production of equal masses of shoots by equal masses of leaves equality of illumination is of special importance. The writer observed deviations from the rule of equal production of shoots by equal masses of sister leaves when the leaves were able to partially cover or shade each other.

TABLE XII

	Shoots produced		Weight of leaves in gm.	Mgm. of shoots pro gm. of leaf
	Number	Weight in gm.		
I. 6 pairs of leaves suspended in moist air				in 30 days
In dark	3	0.016	11.65	1
In light	24	0.543	8.03	68
II. 7 pairs of leaves dipping in water				in 26 days
In dark	14	0.406	13.377	30
In light	17	1.725	17.270	100

In this paper we have considered only the production of equal masses of shoots by equal masses of sister leaves of *Bryophyllum calycinum*. The law is probably correct for leaves of *Bryophyllum* in general, provided a sufficiently large number of leaves are compared, so that the influence of individual differences in the leaves (age, amount of chlorophyll, etc.) is eliminated.

It is also very probable that this form of correlative inhibition of growth is not confined to the leaf of *Bryophyllum*, but is a more general phenomenon. Thus it seems to exist in the potato, where the growth of one bud seems to inhibit the growth of other buds of the same tuber, and perhaps for reasons similar to those set forth here.

Summary

1. Equal masses of sister leaves produce approximately equal masses of shoots in equal time and under equal conditions, even if the number of shoots varies considerably.

2. Those shoots which grow out first attract automatically the material available for shoot formation, thus withholding it from the other buds; the mechanism of this automatic attraction is not yet known.

3. These two factors, the limited amount of material available for growth and the automatic attraction of the material by the buds which grow out first, explain the inhibiting effect of these buds on the growth of the other buds.

4. The relative amount of water in a notch determines which notches give rise to shoots first; by supplying a liberal water supply from without or from within we can determine at will which notches shall grow out first.

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ABNORMALITIES IN NICOTIANA[1]

H. A. ALLARD

(WITH TEN FIGURES)

Synanthic blossoms

Synanthy, or coalescence of blossoms, was noted in a species of tobacco, the seed of which was obtained from South America (S.P.I. no. 33708). This collection of seed gave red, purple, and white-flowered plants. In leaf characters the plants appeared fairly uniform. Although the seed was labeled *N. longiflora*, it may be said that these plants bear no resemblance to that species. They resemble *N. alata* Link and Otto (*N. affinis* Moore) and undoubtedly belong to this species. DEVRIES[2] mentions the occurrence of fasciation in *N. alata*.

The plant which furnished the abnormal blossoms produced beautiful white, exceptionally large blossoms. Three of the more striking abnormalities exhibited different degrees of double-blossom structure. In one instance three blossoms were concerned in the coalescence. These abnormal blossoms were distinguished by the following characteristics (figs. 1, 2, 3):

ABNORMALITY NO. 1.—A union of two blossoms which affected only the corolla tube and calyx. Although the corolla tubes were joined throughout their length, they did not communicate by an opening at any point. In all respects each blossom retained its individuality, possessing the normal number of 5 petals and 5 stamens, one pistil and ovary. In this double-blossom structure the corolla tubes merely adhered, so to speak, along their entire length. The calyx, however, showed a more intimate union, and appeared as one structure with 7 sepals.

ABNORMALITY NO. 2.—In this instance there is but one corolla tube inclosing the stamens, pistils, and the two ovaries. This

[1] Published by permission of the Secretary of Agriculture.

[2] DEVRIES, HUGO, Over de erfelijkheid der Fasciatiën. Bot. Jaarboek (dodoreea) VII. Aug. 1894 (see pp. 94 and 115).

corolla tube, however, is but little larger than the double-tube structure of blossom no. 1. Seven well developed petals were present and 8 filaments bearing anther sacs. One filament was a

FIG. 1.—Side views of abnormal blossoms: *1*, corolla tubes united but not communicating by openings; pistils and ovaries separate in each tube; *2*, single corolla tube inclosing both ovaries and stigmas; *3*, single corolla tube inclosing fasciated pistils and ovaries; ovary walls distinct within; *4*, normal blossom.—T. 1560.

FIG. 2.—Views of abnormal blossoms *1*, *2*, and *3*, looking into throat.—T. 1559

trifle longer and flatter than in the normal blossom, and showed also a double-anther structure. The remaining 7 filaments and anthers appeared normal in all respects. Although this blossom possessed one corolla tube, which was somewhat larger than in the normal blossom, the ovaries and pistils remained distinct, as in blossom

no. 1. The petals were 7 in number, and the calyx possessed 7 sepals.

ABNORMALITY NO. 3.—In this instance the double-blossom structure has affected not only the corolla, but also the ovaries, pistils, and stamens, producing complete fasciation. In size, shape, appearance, and number of petals, the corolla and corolla tube are identical with blossom no. 2. The corolla possessed 7 lobes, and the calyx, similar in all respects to no. 2, possessed 7 sepals. Apparently only 7 stamens are present. One of these unmistakably

Fig. 3.—Corollas of abnormal blossoms *1*, *2*, and *3* removed, showing ovary and pistil structures; *4*, ovary and pistil of normal blossom; *5*, opened corolla of *3*, showing fasciation of pistils and ovary.—T. 1561.

has a double-anther structure. There is some indication of a third anther sac, although this cannot definitely be determined from observation. The filament of this structure was very broad and much flattened throughout. The pistil structure showed a broad, double stigmatic surface, and a broad, much flattened style leading down to a double ovary structure. Although the ovaries were united, each ovary appeared to possess its own walls. In other words, the ovary structure appeared as two closely appressed single ovaries.

ABNORMALITY NO. 4.—In this instance three blossoms are involved in the coalescence (fig. 4). The two blossoms at the right

have a common corolla tube which incloses two separate ovaries, each with its own pistil, as in abnormality no. 2. In this blossom 9 filaments and anthers were also present. The blossom at the left was normal in all respects, except that the corolla tube throughout its length was united with the double corolla tube structure at the right, but did not communicate by an opening at any point. A common calyx possessing many sepal-like divisions inclosed these blossoms. This peculiar blossom formation represents virtually a combination between abnormalities no. 1 and 2.

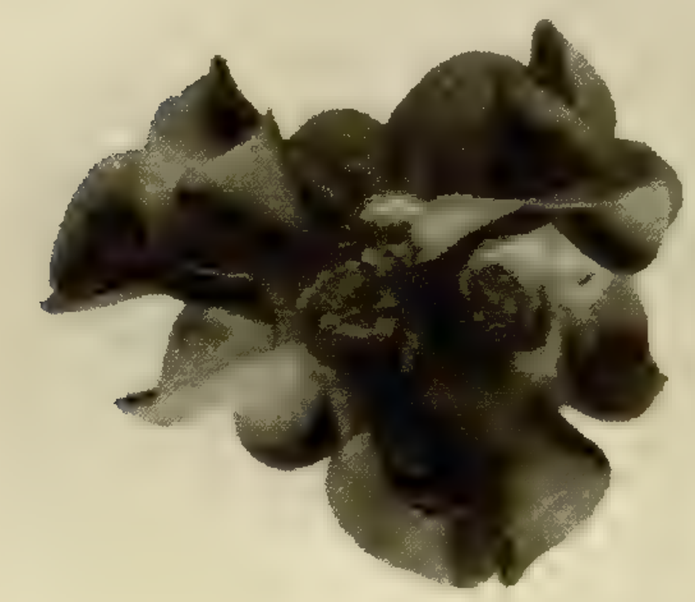

FIG. 4.—Fasciation involving 3 blossoms; union of 2 blossoms at left with common corolla tube inclosing 2 separate ovaries; at right single normal blossom with corolla tube united throughout to double corolla tube structure at left.—T. 1562.

In other plants grown from the same lot of seed, various examples of similar abnormalities in the blossoms have appeared from time to time. In one instance a double-blossom structure appeared as in abnormality no. 2, except that the common corolla possessed 9 instead of 7 lobes; 9 stamens were also present. In other instances showing similar doubling of the blossoms, 11 distinct stamens and 11 distinct corolla lobes were present. Experiments have shown that these abnormalities are more or less hereditary, and, for that reason, the predisposing cause is associated with the germ plasm.

Catacorolla in blossoms of Nicotiana Tabacum as a result of mosaic disease

The blossom abnormality known as catacorolla has received considerable treatment in the literature bearing on teratological phenomena. Catacorolla has been noted in plants of many families. Among the Solanaceae various species of *Nicotiana* have shown instances of catacorolla. PENZIG[3] described and figured

[3] PENZIG, O., Miscellanea Teratologica. Mem. del Reale Instituto Lombardo, 15:147–212. 1884.

instances of catacorolla in *N. Tabacum*, but did not determine its relation to the inherited organization of the plants.

WHITE[4] describes rather fully and illustrates the abnormalities of petalody, pistillody, and catacorolla in certain species of *Nicotiana*. He gives an interesting discussion of the occurrence of catacorolla in F_2 plants of the cross *N. Langsdorfii* and *N. alata*, the parents of which were normal. WHITE found that the type of catacorolla

FIG. 5.—Various phases of catacorolla in *N. Tabacum* produced by mosaic disease; limb of corolla in most instances has undergone excessive development, greatly increasing circumference; although structures simulate doubling in appearance, corolla structure alone is involved, and doubling is only apparent; in fifth blossom (upper row) a very beautiful ascidium or pitcher-like structure is shown.—T. 1704.

with which he worked was hereditary, and in crosses with normal plants it was found to be more or less intermediate in its expression.

Blossom abnormalities associated with fasciation have also been described and illustrated. Some of these resemble very closely certain phases of catacorolla. WHITE[5] describes fasciation

[4] WHITE, O. E., Studies of teratological phenomena in their relation to evolution and the problems of heredity. Amer. Jour. Bot. 1:23–36. 1914.

[5] WHITE, O. E., The bearing of teratological development in *Nicotiana* on theories of heredity. Amer. Nat. 47:no. 565. 1913.

which occurred in Cuban tobacco grown in Cuba. PAOLINI[6] describes and gives an excellent illustration of fasciation occurring in the variety Samsum (*N. Tabacum*), grown in Asia Minor. This is evidently another instance of extreme fasciation similar to that which appeared in the Cuban variety in Cuba. SCARPUZZA[7] described and illustrated fasciation similar to that observed by PAOLINI.

FIG. 6.—Catacorolla in *N. Tabacum* produced by mosaic disease; in most instances development has been suppressed in these blossoms; ascidia shown in third and fifth blossoms (upper row); last blossom in lower row shows tendency toward fasciation; 2 blossoms, one nearly normal, another abnormal, are inclosed in common calyx.—T. 1576.

During the writer's investigations of the mosaic disease of tobacco, catacorolla has been one of the most common abnormalities produced in the blossoms of *N. Tabacum* in connection with the

[6] PAOLINI, V., Caso di Concrescenza in una Pianta di Samsum. Boll. Tecnico del R. Instituto Sperimentale in Scafati (Salerno). **6**:no. 4. 1907.

[7] SCARPUZZA, A., Di Alcune Anomalie Morfologiche su Piante di Aya Solouc. Boll. Tecnico del R. Instituto Sperimentale in Scafati (Salerno), anno VI, no. 4; July–August, 1907.

disease. All phases of catacorolla have been noted. Very frequently the normal development of the corolla has been considerably exceeded, producing large and very showy blossoms, with a much folded and greatly increased circumference or border (fig. 5).

Although the tobacco blossom is normally gamopetalous, the parts of the corolla may be more or less completely separated by clefts into petaloid segments. In some instances these have been replaced by very striking and beautiful ascidia or pitchers, borne

FIG. 7.—Abnormal blossoms of *N. Tabacum* produced by mosaic disease of tobacco; corolla development has been almost completely suppressed; in blossom at left pistil shows peculiar twisted structure; in blossoms at right, representing the 5 corolla lobes normally present, stamens and pistils are normal in development; hairy portion of filaments in normal blossoms is adnate to corolla tube.—T. 1598.

upon long, slender, tubular stalks (see fifth blossom, top row, fig. 5, and third and fifth blossoms, top row, fig. 6). The blossom at the right in fig. 7 shows a complete separation of the corolla into 5 distinct and nearly equal petaloid segments. In this blossom the normal development of the stamens and pistils has been but little, if at all, interfered with. Although nothing is known concerning the development of the various structures of the flower in connection with the mosaic disease, it appears that disturbances in the petal primordia are more likely to occur than in the primordia of other structures.

Although the mosaic disease of tobacco may produce all phases of catacorolla in the blossoms of *N. Tabacum*, other species rarely, if ever, show this abnormality in connection with the mosaic disease. Although petunias, *Datura Stramonium*, *Nicotiana glauca*, *N. longiflora*, *N. silvestris*, *N. alata*, etc., are readily infected with the mosaic disease of tobacco, the writer has never observed the occurrence of such abnormalities in the blossoms of these plants affected with the mosaic disease.

FIG. 8.—Plant of first generation of cross Maryland Mammoth (♀) × Yellow Pryor (♂), showing development of growing points; character appeared in many plants of first generation of this cross; plant shown was grown in 8 in. pot; taller branch is 28 in. high; smaller 21 in. in height.—T. 1602.

Likewise, the blossoms of *N. glutinosa* affected with a mosaic disease similar to but not identical with the mosaic disease of tobacco have never yet shown the catacorolla abnormality. It is interesting to note, however, that first generation plants of the cross *N. Tabacum* (♀) × *N. glutinosa* (♂) show all phases of catacorolla when affected with the mosaic disease of *N. glutinosa*, to which these hybrids are susceptible. These facts indicate that catacorolla is more readily induced by the mosaic disease in blossoms of *N. Tabacum* than in many other species of *Nicotiana*.

Normal blossoms and abnormal blossoms showing all degrees of catacorolla may frequently be shown on the same branch of the inflorescence. Although the inciting cause is associated with the mosaic disease of tobacco, conditions which disturb normal growth, such as cutting back, starvation, etc., tend to accentuate the expression of the abnormality.

WHITE'S observations show that catacorolla may sometimes appear suddenly in connection with a cross and persist in the

hereditary mechanism of the tobacco plant. The writer's experiments show that catacorolla originating as a result of the mosaic disease of tobacco is not inherited. For this reason the causal factor is external or accidental in its nature, and does not extend its influence to the constitution of the germ plasm. Although it has not been definitely established that the primary cause of the mosaic diseases affecting *N. Tabacum* and *N. glutinosa* is parasitic

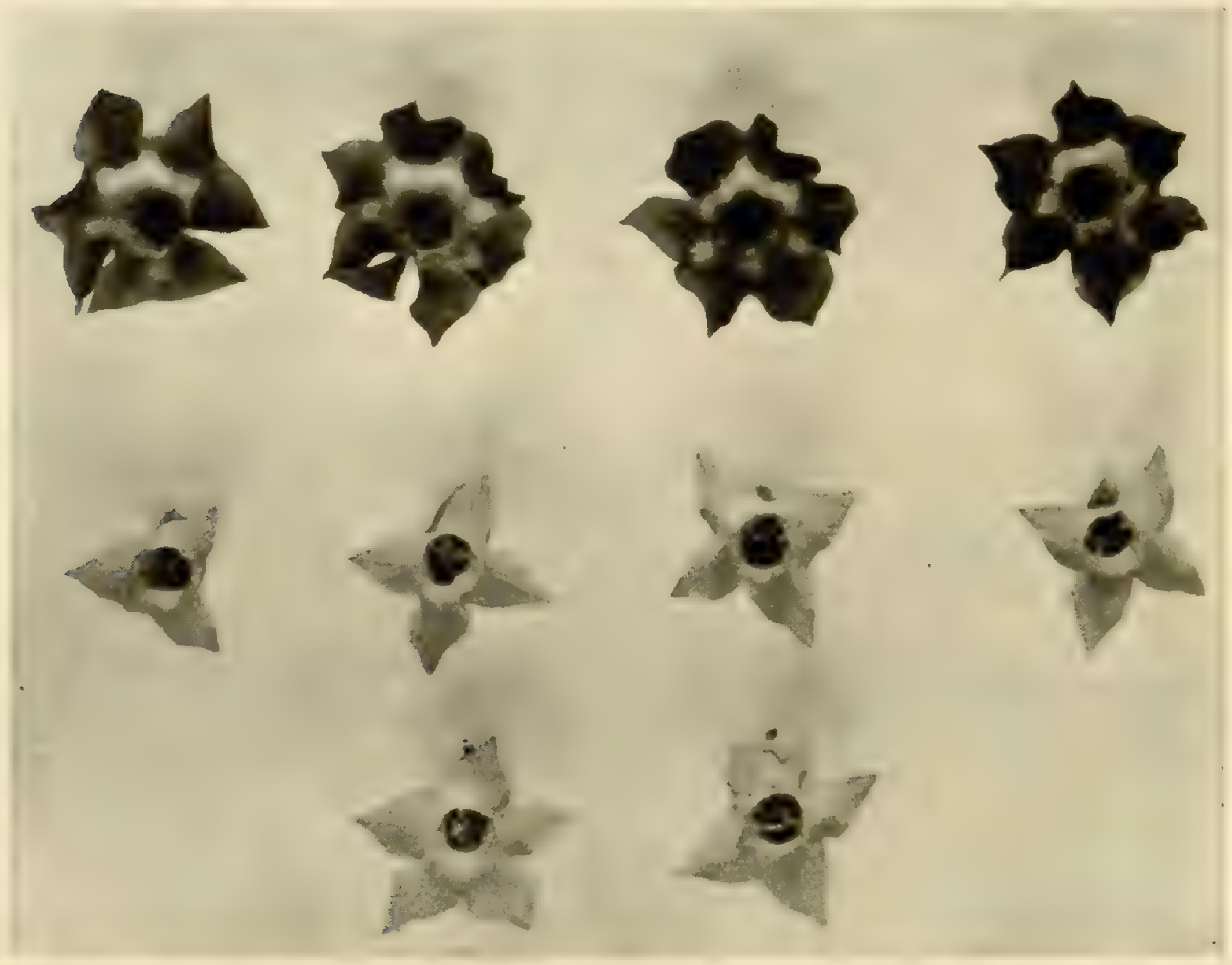

FIG. 9.—Upper row: blossoms possessing 6 and 7 corolla lobes; middle row: blossoms with 3 and 4 corolla lobes; lower row: normal 5-lobed blossom at left, abnormal blossom at right.—T. 1763.

in its nature, it is evident that the blossom abnormalities observed in *N. Tabacum* as a result of the mosaic disease are analogous in their origin to the abnormalities, monstrosities, galls, etc., due to insects, fungi, bacteria, etc.

The development of two growing points

In the cross Md. Mammoth (♀) × Yellow Pryor (♂), a number of young plants of the first generation were characterized by two

growing points (fig. 8). These were evident when the plants were very small. As the plants became older, one of the growing points was not infrequently outgrown by the stronger branch. In other instances the two growing points maintained almost equal vigor, producing two well developed stalks which finally blossomed. In the Maryland Mammoth variety there seems to be a tendency to develop bifurcation of the main stem in a small percentage of the plants. This feature, however, has usually made its appearance rather late in the development of the plant.

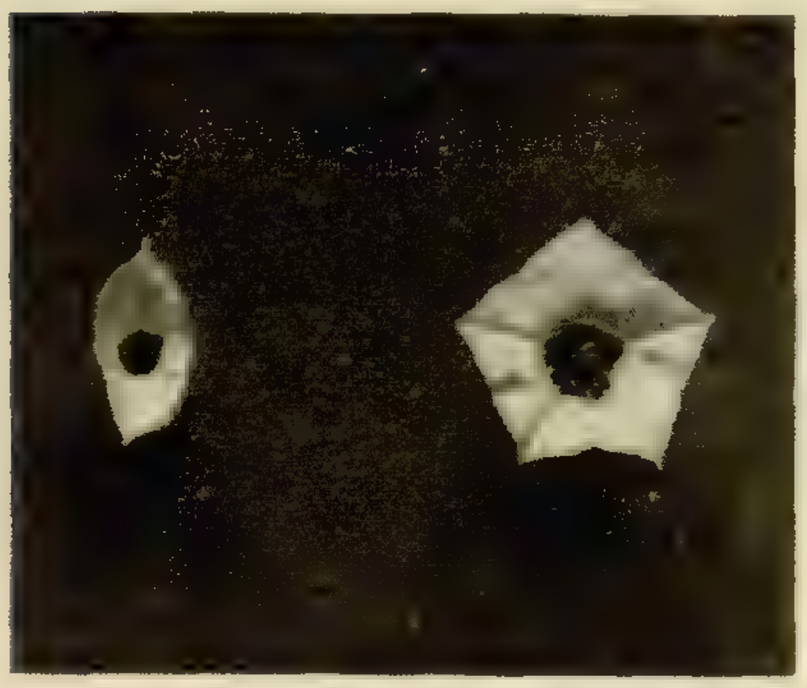

FIG. 10.—*N. Tabacum*, showing abnormal form at left, with only 2 petals; normal blossom with 5 petals from same plant shown at right; this singular blossom occurred on a plant of second generation of a cross between 2 distinct varieties of *N. Tabacum*, and was the only abnormal blossom produced by plant.—T. I. 2188.

Corolla lobes abnormal in number

In the normal tobacco blossom the corolla has 5 lobes and 5 stamens. In abnormal blossoms the number of corolla lobes may be greater or less than the normal number. Blossoms abnormal with respect to the number of corolla lobes are shown in figs. 9 and 10. The blossoms in the top row (fig. 9) were obtained from a plant of the second generation of the cross *N. Tabacum* (♀) × *N. silvestris* (♂), and were a deep red. Nearly all the blossoms produced by the plant possessed 6 or 7 corolla lobes. A few normal blossoms were produced. The plant was grown in an 8-inch pot and appeared to be normal in all respects.

The blossoms shown in fig. 9, rows 2 and 3, were obtained from a single plant of ordinary tobacco (*N. Tabacum*) and were pink in color. Although a few blossoms possessed the normal number of corolla lobes (5), the majority possessed only 3 or 4 lobes. The plant producing these blossoms showed typical symptoms of "Frenching," which appears to be a nutritional disturbance associated with unfavorable soil conditions. This plant was grown in an 8-inch pot.

An examination of the blossoms showed that the number of stamens in most instances was the same as the lobes of the corolla. The relations are given in table I.

TABLE I

Blossom no.	Row	Corolla lobes	Stamens	Result
1 (red)	Upper	7	7	Calyx and pistil normal
2 "	"	7	6	" " " "
3 "	"	6	6	" " " "
4 "	"	6	6	6 calyx lobes, pistil normal
5 (pink)	Second	3	4	Calyx and pistil normal
6 "	"	4	4	4 calyx lobes, pistil normal
7 "	"	4	4	" " " " "
8 "	"	4	4	" " " " "
9 "	Third	5	5	Blossom normal in all respects
10 "	"	4	4	Calyx and pistil normal

In blossom no. 10 a small, slender division was also evident in addition to the 4 large, equal lobes. In all the blossoms the stamens present were normal in their development.

In fig. 10 a blossom with a 2-lobed corolla is shown in comparison with a normal, 5-lobed blossom of the same plant. This 2-lobed blossom occurred on a plant of the second generation of a cross between two distinct varieties of *N. Tabacum*, and was the only abnormal blossom produced on the plant.

Bureau of Plant Industry
Washington, D.C.

CHANGING DIATOMS OF DEVILS LAKE

CLARENCE J. ELMORE

During the summer of 1915 I spent some time at the Biological Station of the University of North Dakota at Devils Lake, investigating the diatoms of the lake. Before this considerable diatom material had been sent to me by Dr. R. T. YOUNG of the University, who is conducting the biological survey of the lake.

The immediate practical object in the survey is to determine the organisms in the lake in relation to the fish that might be able to subsist upon them, and diatoms being the most abundant of microscopic plants, deserve special attention in this connection. At present the stickleback, *Eucalia inconstans*, is the only species of fish in the lake, notwithstanding the fact that food is abundant. This species, however, is common.

The lake is passing through a rapid transition. It was formerly a fresh-water lake fed by streams, and at that time it contained large numbers of fish, but the lake is rapidly becoming lower. From 1883 to 1912 it fell 14 ft., a fall of about half a foot a year. It has now no apparent inlet or outlet, and the water is becoming salt. The salinity, however, is quite different from that of sea water. It differs somewhat in different parts of the lake and at different seasons of the year, but the following analyses made by Dr. F. H. HEATH of the University of North Dakota in the summers of 1914, 1915, and 1916 will give a general idea of the condition of the water. No complete analysis was made in 1915, but the total amount of solids in that year was greater than in 1914 or 1916, due to the lower level of the water.

	1914	1915	1916
Carbonate (CO_3)	254	213	.....
Bicarbonate (HCO_3)	447	639	.....
Silica (SiO_2) variable	370	.....	242 and 69
Sulphate (SO_4)	6231	.....	6706
Fe_2O_3 and Al_2O_3	.....	.....	121
Calcium (Ca) variable	.....	.....	86.5
Magnesium (Mg)	598	.....	579
Chlorine (Cl)	1106	.....	1284
Total solids	11,980	14,477	13,020

These analyses show about 1 per cent of solids in the lake, or about one-third of the amount in ocean water. This comparatively rapid increase in salinity has produced a corresponding change in the diatoms of the lake, as well as in all the other organisms that it contains. We have no knowledge of what diatoms were in the lake when the water was fresh, but we can safely assume that they were all of species commonly found in fresh water elsewhere, perhaps the same as in Court Lake, a fresh-water lake which was formerly a part of Devils Lake.

In my work I identified 56 species of diatoms in the lake. Of these, 25, as reported elsewhere, are genuine fresh-water species; 20 are species that are found in either fresh or brackish water; 3 are in brackish water only; 2 are reported as being found in fresh, brackish, or salt water; 2 in brackish or salt water; and 4 as marine only. It is possible that when the water in the lake was fresh 50 of these species, that is, all but the 4 marine ones and the 2 that are brackish or marine, were living in it; however, this is not likely. It is probable that there was then a much larger proportion of fresh-water species, as there usually is in fresh water, and fewer of those of varied habitat. As the water became more saline, however, diatoms adapted to either fresh or brackish water gained a foothold, then those adapted to either brackish or salt water, and finally the 4 marine species. One of these marine species, *Chaetoceros elmorei* Boyer, classed as marine because the genus is a marine one, was identified by C. S. BOYER as a new species. It is not likely, however, that it originated in this lake, and it is probably to be found elsewhere.

The importation of marine species so far inland is easily accounted for. It would be perfectly possible for them to be carried in the air, but adhering to migratory birds is a much more probable explanation.

The 25 species of fresh-water diatoms present the greatest anomaly. There is nothing in their appearance to indicate that they have been in any way modified by their changed environment.

There are several smaller lakes in the vicinity of Devils Lake which were formerly part of the main lake, but have been separated from it by the lowering of the water. The analysis of the water

made in 1916 by HEATH shows the total solids in the main lake to be 13,020, or about 1.3 per cent; in Minnewaukon Bay above the grade, 0.4464 per cent; Court Lake, 0.12 per cent; and Lake I, 0.1328 per cent. The water in all of these lakes shows the same large amount of magnesium sulphate.

These conditions of salinity are correlated with interesting differences in the diatoms. The portion of Minnewaukon Bay from which the sample was taken was formerly part of the main lake and its water had about the same degree of salinity. But within the past year a highway grade has been made, cutting it off, and it is now connected with the main lake only by a culvert. Through this culvert the main lake receives about 2,000,000 gallons of water daily. This leaves the water in the bay practically fresh. In a collection made in this bay 14 species of diatoms were found, all but one of which are also found in the main lake. This one species, *Stephanodiscus niagrae*, is a fresh-water species. In this case a change in the condition of the water of from 1.3 per cent to 0.4464 per cent of solids has in one season made practically no change in the diatoms.

Lake I contains 0.1328 per cent of solids, or about one-third as much as Minnewaukon Bay. Instead of having been separated from the main lake only a few months, as in the case of Minnewaukon Bay, it has been separated for about 5 years. In this lake 24 species were found, 6 of which are not found in the main lake. These 6 are all fresh-water species.

Court Lake contains 0.12 per cent of solids, nearly the same as Lake I, but of the 22 species of diatoms found in it, 13 are not found in the main lake, and all of these 13 are fresh-water species; but Court Lake has been separated from the main lake for about 100 years. Since the main lake became salt, Court Lake has not been connected with it. These 13 species not found in the main lake, therefore, may have been originally in it and have died out on account of the saltness of the water; or they may have been introduced into Court Lake after the separation; or, what is more likely, some may have been in the original lake and others have been introduced later.

The fact that little change has been made in the diatoms by the change of water in the branch of Minnewaukon Bay would indi-

cate that diatoms are not very sensitive to such changes. Also, the fact that Lake I, which contains about the same amount of solids as Court Lake, but has recently been connected with the main lake, has a diatom flora much more like the main lake than like Court Lake, also indicates that diatoms are slow in responding to changes in environment.

No marine species were found in any of the outlying lakes, but as they are comparatively rare in the main lake, and the other lakes have been less carefully explored, this fact probably has no significance. More careful collecting may show them there also.

In a spring at Sully's Hill on the shore of the lake, but at an elevation of 50 ft. or more above it, 9 species were found, 3 of which were found in the lake and 6 not found in it. These probably have no relation to the diatoms of the lake, for there has never been any connection between the water of the two places, and these diatoms are all of species found commonly in fresh water everywhere.

In ditches along railroads and in pools 26 species were found, 17 of which were found in the main lake and 9 of which were not. The composition of the water in these places varies greatly. After rains, when they are filled, the water is practically fresh, but as it evaporates it becomes considerably concentrated. This, together with the fact that this land was once covered by the lake, explains the presence of the forms commonly found in brackish water. Some of these facts are summarized in following table I.

TABLE I

Place	Species in main lake	Not in main lake	Percentage of solids	Time separated from main lake	Habitat as reported elsewhere					
					Fresh	Marine	Fresh and brackish	Brackish	Marine or brackish	Fresh, brackish, or marine
Main Lake.....	56	0	1.3	.....	25	4	20	3	2	2
Minnewaukon Bay.....	13	1	0.4464	6 months	6	1	6	0	0	1
Court Lake.....	9	13	0.12	100 years	16	0	4	1	1	0
Lake I.....	18	6	0.1328	5 years	12	0	10	1	1	0
Pools and ditches	17	9	.....	.....	14	0	1	3	1	2

The diatoms of this region illustrate what has commonly been observed elsewhere, that many of them adapt themselves readily

to changes in environment. Here there are marine and fresh-water species living together under semimarine conditions, and in Minnewaukon Bay, where the water changed from saline to fresh, the diatoms that had been living in the saline water seemed to have been in no way affected in one season by the change. In Court Lake, the water of which has never been salt, there is one species whose habitat is reported as "marine or brackish." Its presence here may be explained by the nearness of Court Lake to salt water, making it easy for it to be introduced; and its continuing to live there may be explained by its adaptability to various environment.

Should the lake continue to diminish in size, its salinity will probably increase; and at the same time other bays will be cut off and become separate lakes. These changes will furnish interesting material for study, not only of the diatoms, but of all other organisms inhabiting the lake.

GRAND ISLAND COLLEGE
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BRIEFER ARTICLES

REGENERATION OF BRYOPHYLLUM CALYCINUM

(WITH TWO FIGURES)

In two articles on regeneration of *Bryophyllum*, LOEB[1] bases his theories of inhibition and correlation in the regeneration of *Bryophyllum* upon the results of numerous experiments with severed leaves and portions of stems, and upon the negative results obtained with "normal plants." After reading these articles, the writer recalled numerous instances of regeneration seemingly at variance with the experiments described.

Experiments by LOEB indicate that under suitable conditions whole leaves severed from the plant produce shoots from only a few notches. The writer has found the number of notches which produce shoots to vary from one or two to all of the notches, when whole leaves were placed in the moist air of a Wardian case, or, more frequently, on damp soil in the garden. The growth of all or many notches of whole leaves does not coincide with LOEB'S results, and furthermore is in direct opposition to his theory of the flow of certain substances in the leaf determined by the first notches which begin to grow, and the consequent inhibitory effect produced upon the growth of other notches. In view of LOEB'S results and theories, more striking even than the growth of many notches on severed leaves is the production of roots and shoots in the notches of leaves attached to growing plants. In introducing his subject, LOEB asks, "Why does a leaf not form roots and shoots in its notches so long as it is in connection with a healthy plant?" (*loc. cit.* **60**:250). And again, under theoretical remarks, "When a plant is normal, it is almost or possibly absolutely impossible to induce the notches of a leaf which is connected with the plant to grow" (*loc. cit.* **60**:274).

Pot-grown plants of *B. calycinum* in the writer's possession have frequently grown both shoots and roots from leaf notches while the leaves were in connection with the plant. Early in the spring of 1917 a large plant of *Bryophyllum* (fig. 1) began to produce shoots from the leaves

[1] LOEB, JACQUES, Rules and mechanism of inhibition and correlation in the regeneration of *Bryophyllum calycinum*. BOT. GAZ. **60**:249–276. 1915; Further experiments on correlation of growth in *Bryophyllumca lycinum*. BOT. GAZ. **62**:293–302. 1916.

more abundantly than the plants often do. The accompanying photographs were taken May 12, when shoot production had reached its maximum. It was not necessary to induce the notches to grow; they grew freely under ordinary room conditions, and with only the usual attention which a pot plant in a residence receives.

A number of the leaves of the plant (fig. 2) produced shoots from all the notches or from all except the basal notches, a phenomenon which, to accord with LOEB's theories, should take place only under very special conditions. The plant appears to be a "healthy plant," as healthy and

FIG. 1

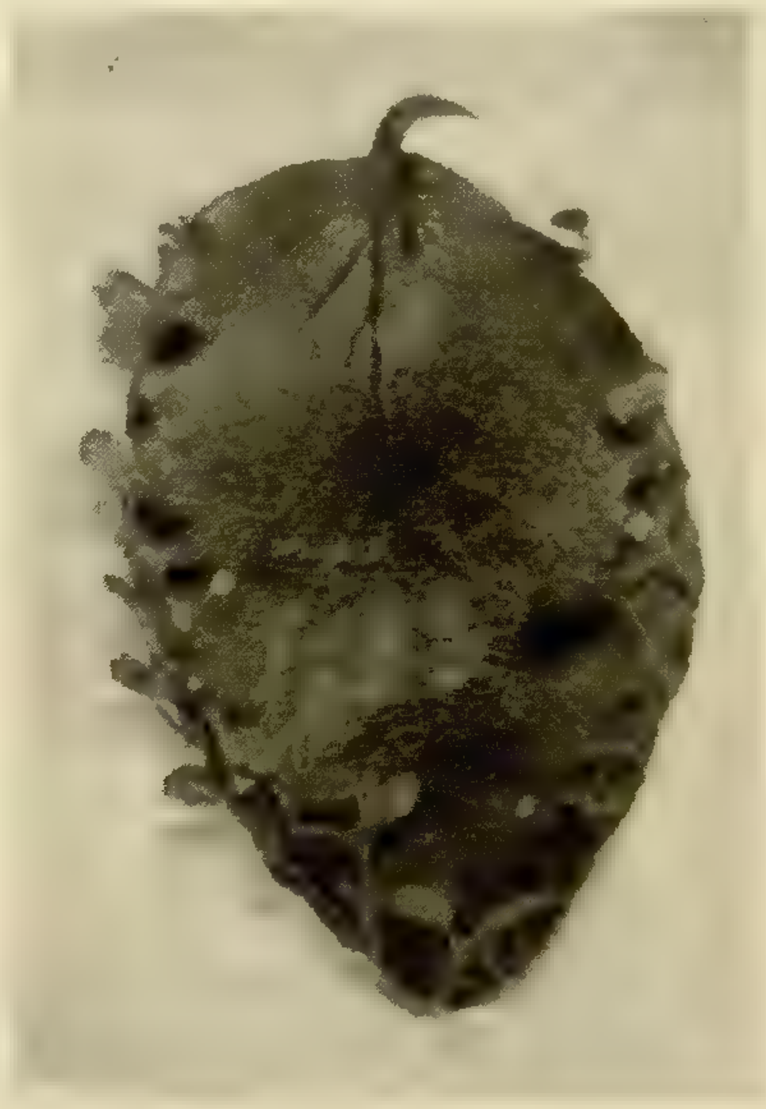

FIG. 2

FIGS. 1 AND 2.—Fig. 1, large pot-grown plant of *Bryophyllum calycinum* producing shoots from many of its leaves; fig. 2, leaf of plant shown in fig. 1, with shoots growing from all except the two small basal notches.

vigorous a plant as the writer has ever seen. Whether or not it is a "normal plant," as a normal plant is conceived of by LOEB, is difficult to say, for nowhere does he define a "normal plant." He does state: "If, however, the flow of substances in a plant is abnormal, either because the roots or the apical parts or both have suffered, a growth of shoots may occur in moist air from the notches of leaves which are in contact with the plant." There is no indication that either the roots or the apical parts have suffered; the plant appears healthy, and has had no accident.

A "normal plant" will probably be interpreted to be a "healthy plant," inasmuch as these two terms are used interchangeably in con-

nection with statements concerning the growth of notches of leaves attached to plants. It would seem, therefore, that the conclusions reached by LOEB are not substantiated by the behavior of the plants in question.—E. LUCY BRAUN, *University of Cincinnati.*

MISTLETOE VS. MISTLETOE

(WITH ONE FIGURE)

The specimen shown in fig. 1 was collected near Tucson about three years ago by Professor J. J. THORNBER of this University. *Phoradendron flavescens*, the larger plant, acting both as partial parasite and host, is found on species of *Quercus*, *Fraxinus*, and *Juglans;* while *P. californicum*, the smaller one, is a common parasite on *Parkinsonia*, *Prosopis*, and *Acacia*. Although the mistletoe is of common occurrence on palo verde and mesquite in this region, the writer has never before seen one species parasitic on another. It is interesting to consider water and salts, and possibly other materials, as having to pass successively through the vascular systems of three different plants before they reach the cells wherein they enter into metabolic activities. With transpiration much stronger in *P. flavescens* because of its larger transpiring surface, it would appear as if the second species must have a rather difficult time in securing a sustaining share of the ascending stream of sap. Possibly physiologists could find a higher osmotic pressure in the smaller species to account for its ability to maintain an existence in its peculiar location.—J. G. BROWN, *University of Arizona.*

FIG. 1.—*Phoradendron californicum* parasitic on *P. flavescens*.

CURRENT LITERATURE

MINOR NOTICES

A textbook of botany.—The second part of GANONG'S *Textbook of Botany* has appeared,[1] including a presentation of the plant groups, and also the ecological classification of plants. In the first chapter the phylogenetic connections of the major plant groups are presented; while the subsequent chapters give a general account of the different groups, using selected forms as illustrations. The author is so well known as a teacher that it is hardly necessary to say that the presentation, following the thought he has had in mind, is thoroughly well done.—J. M. C.

Manual of woody plants.—TRELEASE[2] has published a small pocket manual of the woody plants used for decorative purposes. The intention of the author "is to make it possible for any careful observer to learn the generic and usually the specific name of any hardy tree, shrub, or woody climber that he is likely to find cultivated in the United States." The book contains 782 species in 247 genera. Its keys and descriptions, with the help of the glossary, should enable those untrained in botany to recognize woody plants under cultivation in parks and other ornamental grounds; while its size makes it available as a pocket companion.—J. M. C.

The sweet pea.—The rapid advance in plant pathology is bringing forth popular books on the diseases of special crops for the use of commercial growers. These works in order to meet the demand of the growers must be broader than most Experiment Station publications. The most recent publication of this kind is by TAUBENHAUS,[3] whose studies in the Delaware Agricultural Experiment Station have given him an especially good preparation for this work. The book gives a review of the history, evolution, and classification of sweet peas; a thorough discussion of cultural methods; and the diseases (including insect pests) and methods for their control. The work is very carefully prepared and well illustrated, and the discussions so clear and concise that the grower will find it very helpful.—MEL. T. COOK.

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[1] GANONG, WILLIAM F., A textbook of botany for colleges. Part II. 8vo. pp. ix+391–595. *figs. 275–400.* New York: Macmillan. 1917. $1.00.

[2] TRELEASE, WILLIAM, Plant materials of decorative gardening: The woody plants. 16mo. pp. 204. Urbana: Published by the author. 1917.

[3] TAUBENHAUS, J. J., The culture and diseases of the sweet pea. New York: E. P. Dutton & Co. 1917.

Botany of crop plants.—ROBBINS[4] has written a most successful botanical textbook with a direct bearing on agriculture, and it will be welcomed by many teachers in botany. The work is the outcome of a course in Freshman botany which the author has been giving for several years, and is intended for both agricultural and non-agricultural schools. It is divided into two parts. The first part consists of 8 chapters and includes general or fundamental botany. It is devoted entirely to angiosperms and would be somewhat better for a college textbook if more extensive. The second part gives excellent discussions of most of our important agricultural crops, including general descriptions of the plants, their flowers and fruits, with discussions of their history, uses, and distribution. Some of these discussions include maps and keys. Each chapter closes with an excellent bibliography. The value of the book would be greatly increased by laboratory outlines, by chapters on lower plants in the first part, and by chapters on plant breeding, forestry, plant pathology, and other related subjects in the second part.—MEL. T. COOK.

NOTES FOR STUDENTS

Addisonia.—The third number of the second volume of this journal contains colored plates and popular descriptions of *Harrisia gracilis*, *Epidendrum oblongalum*, *Aesculus parviflora*, *Micrampelis lobata*, *Bomarea edulis*, *Aster tataricus*, *Pachyphytum bracteosum*, *Harrisia Martini*, *Oncidium pubes*, and *Raphiolepis ovata*.—J. M. C.

Subalpine plants of the Rocky Mountains.—Continuing his series of studies of the flora of the Rocky Mountains already noted,[5] RYDBERG[6] has made an analysis of the vegetation of the subalpine zone. Lists of species found in the different formations are given, and three classes are distinguished according to whether the plants are restricted to the northern or to the southern Rockies, or are common to both.—GEO. D. FULLER.

Revegetation of Taal volcano.—Swept bare of plants by an eruption in 1911, the slopes of Taal volcano have afforded an excellent opportunity for the study of revegetation within the tropics. Records by GATES[7] show that the grasses are prominent among the pioneers, followed by shrubs and small trees. In contrast with the conditions at Krakatau, ferns are found to be

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[4] ROBBINS, W. W., Botany of crop plants. Philadelphia: P. Blakiston's Sons. 1917.

[5] BOT. GAZ. **62**:83–84. 1916; **63**:423–424. 1917.

[6] RYDBERG, P. A., Phytogeographical notes on the Rocky Mountain region. VII. Formation of the subalpine zone. Bull. Torr. Bot. Club **44**:431–454. 1917.

[7] GATES, F. C., The pioneer vegetation of Taal volcano. Phil. Jour. Sci. **9**:391–434. 1914.

———, The revegetation of Taal volcano, P.I. Plant World **20**:195–207. 1917.

relatively unimportant. Lists of species present three and four years after the eruption are given.—GEO. D. FULLER.

Soil moisture.—The increasing demand for the use of quantitative studies of soil moisture in ecological and agricultural studies makes ALWAY'S[8] investigation of methods for the accurate determination of the hygroscopic coefficient very timely. HILGARD'S method is found to give reliable results, but certain changes in details of manipulation are found to be desirable as matters of convenience. Two important conclusions are that the amount of hygroscopic moisture absorbed increases with rise of temperature, and that 12 hours' exposure to saturated atmosphere is sufficient, provided the soil layer is very shallow.—GEO. D. FULLER.

A new disease of wheat.—SMITH[9] has announced the appearance in the Middle West of a new disease of wheat, which he says "is a matter of much concern." The disease has been known since 1902, but the destruction of winter wheat in 1917, which has generally been ascribed to winter-killing, led to the suspicion that a part of the loss might be due to this new disease. It is believed to be of bacterial origin, and promises to be difficult to control.

The disease attacks not only the leaves, glumes, awns, rachis, and stalk, but sometimes also the kernel itself, suggesting that it is carried over from year to year on the seed.—J. M. C.

Vegetation of Colorado.—A valuable bulletin by ROBBINS[10] is a continuation of his work on the vegetation of Colorado in its relation to climate.[11] Comprehensive tables show what is known about the climates of the state as to temperature, precipitation, frost, humidity, length of growing seasons, etc. Following the statistical matter is a brief account of the chief types of vegetation and their relation to agriculture, under the following headings: grass-steppe, shrub-steppe, chaparral, pinyon pine-juniper woodland zone, yellow pine forest zone, lodgepole pine forest zone, white fir forest zone, Engelmann spruce forest zone. Maps and charts are freely employed. Useful lists of the more important trees, shrubs, and herbs are given. Publications such as this for other states would be of great value to botanists as well as to farmers.—. FRANCIS RAMALEY.

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[8] ALWAY, F. J., and others. Some notes on the direct determination of the hygroscopic coefficient. Jour. Agric. Research **11**:147–166. 1917.

[9] SMITH, ERWIN F., A new disease of wheat. Jour. Agric. Research **10**:51–53. *pls. 4–8.* 1917.

[10] ROBBINS, WILFRED W., Native vegetation and climate of Colorado in their relation to agriculture. Bull. no. 224 Colo. Agric. Exper. Sta., Ft. Collins, Colo. 1917.

[11] BOT. GAZ. **49**:256–280. 1910.

Cleistogamy in Heteranthera.—WYLIE[12] has discovered that *Heteranthera dubia* is cleistogamous, and his investigation of the situation has led him to some interesting conclusions and questions. As he remarks, this plant "has developed a vegetative body well adapted to the submersed life, as shown by its vigorous and successful growth. It has failed, however, to attain floral specialization adequate to insure cross-pollination." He finds that there is no possibility of cross-pollination, except through flower elongation, "so that if seeds are to be set with certainty and in considerable numbers, it must be through close pollination under water, excepting the relatively few flowers so situated that they can reach the air, and these also seem to have acquired the habit of self-fertilization." He suggests that this species is a favorable one for experimental study in plant-breeding, since it grows readily, and if kept submerged sets seeds freely without further attention.—J. M. C.

A living physical system.—BRIGGS'S[13] clear-cut picture of the living plant as a physical system which is absorbing energy and performing useful work is significant of the present trend of botanical thought. He suggests that the doctrine of vitalism is being restricted more and more as our knowledge of plant phenomena increases. He summarizes the situation as follows: "The mechanism of plant processes, not at present explainable on a physico-chemical basis, would be termed by the vitalistic school as 'vital,' by the physico-chemical school as 'unknown.'" He treats the subject under the following heads: (1) the efficiency of the plant system, (2) the growth rate, (3) gas exchange between the leaf and the air, (4) diffusion through perforate septa, (5) the ascent of sap. In closing he emphasizes the fact that as a means of efficiency in plant production it is important to have the fullest possible understanding of the physical and chemical processes associated with growth.—GEO. B. RIGG.

Leaf duration in evergreens.—In studies embracing 9 gymnosperms and 22 angiosperms, growing in the state of Washington, PEASE[14] has investigated the duration of leaves and has endeavored to account for the variations displayed. The leaf age limit reaches from about a single year in *Rhamnus Purshiana* to 23 years in *Taxus brevifolia*. From determinations upon approximately 100 twigs of each species grown under a variety of conditions, graphs are plotted showing the range for each. Some of the factors found to be efficient in affecting duration are (1) age, mature trees having older leaves;

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[12] WYLIE, ROBERT B., Cleistogamy in *Heteranthera dubia*. Bull. Lab. Nat. Hist. State Univ. Iowa 7:48–58. 1917.

[13] BRIGGS, LYMAN J., The living plant as a physical system. Jour. Wash. Acad. Sci. 7:89–111. 1917.

[14] PEASE, VINNIE A., Duration of leaves in evergreens. Amer. Jour. Bot. 4:145–160. *figs. 12.* 1917.

(2) shade, increasing permanency; (3) wind, tending to decrease duration; (4) moisture, tending to lengthen duration; and (5) bog habitat, causing the same early fall as dry habitat. In general, factors which cause increase in transpiration are accompanied by decrease in leaf duration, while those factors tending toward decrease in photosynthetic activity are accompanied by increased duration. The author of the paper is to be commended upon its good organization.—GEO. D. FULLER.

Physical factors in plant distribution.—The recent advances along the line of devoting more attention to the factors controlling vegetation and the progress made in more correctly evaluating these factors have been discussed by SHREVE,[15] who has also pointed out the striking contrasts in the physical conditions of mountains in humid and arid regions.[16] The contrasts in humidity are most marked, but are manifest also in temperature and light. Examples are seen in the Blue Mountains of Jamaica, with a daily temperature range of 6–10°, compared with the Santa Catalina Mountains of Arizona, with a daily range of 40–65° and corresponding annual amplitudes. These and other differences enumerated result in plant associations where a stratified rain forest in the former region, with large trees, under trees, shrubs, large herbs, and small hygrophilous plants superimposed in luxuriant profusion, contrasts with the scanty shrubs, the open pine forests, and somewhat denser fir forests, all almost devoid of any stratification whatever, which are distributed over the slopes of the latter.—GEO. D. FULLER.

Anatomy of Betulaceae.—The intensive anatomical work among the gymnosperms has forged an unusually effective weapon for attacking phylogeny, and it is beginning to be used in the interpretation of angiosperms, with very interesting results. HOAR[17] has investigated the anatomy of the Betulaceae and has come to the conclusion that the group belongs "near the base of the dicotyledons," and that *Alnus* most clearly illustrates the primitive conditions. In this genus the aggregate condition of rays is either normally developed or in a state of reduction, while in the more advanced genera (*Carpinus*, *Ostrya*, and *Betula*) the aggregate condition persists only in conservative regions or is "recalled by injuries." The conclusion of course depends upon the position of the aggregate ray in the phylogenetic series of ray structures. In the same connection *Casuarina* was investigated, the result being to confirm its low position among the dicotyledons, and also its close anatomical relation-

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[15] SHREVE, FORREST, The weight of physical factors in the study of plant distribution. Plant World **19**:53–67. 1916.

[16] ———, The physical control of vegetation in rain forest and desert mountains. Plant World **20**:135–141. 1917.

[17] HOAR, CARL S., The anatomy and phylogenetic position of the Betulaceae. Amer. Jour. Bot. **3**:415–435. *pls. 16–19.* 1916.

ship with the Amentiferae. In fact, this relationship is one argument for the primitive character of the Amentiferae.—J. M. C.

Translocation of sugar.—MANGHAM[18] has attempted to show that adsorption in the complex colloidal system of the protoplasm may play an important rôle in the translocation of sugar in the plant. The discussion is purely hypothetical, and it is rather hard to see how the main hypothesis is to be put on an experimental basis. A quotation from his summary will show the line of his reasoning.

Adsorption compounds of albumen, lecithin, and glucose are known. It is suggested that in vegetable protoplasm there are present constituents capable of adsorbing sugars from solution. For any given concentration of sugar present in the liquid phase of the protoplasm, and the cell sap continuous with it, there would be a definite concentration of sugar present at the adsorbing surface. Any alteration of concentration in either region would lead to a readjustment of concentration equilibrium, which would be propagated as a wave through the system composed of the adsorbing particles and the solution immediately in contact with them. The rate of propagation of this wave would depend very much upon the degree of approximation of the particles under consideration, and would increase as the distance between them decreased. Connecting threads are assumed to provide a continuous protoplasmic pathway, though they impose restrictions varying with their frequency and tenuity.

Diffusion is generally recognized as being too slow to account for the considerable movement of sugars and other materials in plants. There must be mass movement to supplement molecular movements. MANGHAM's hypothesis does not help us out in this respect because it must assume that "readjustment of concentration equilibrium" is brought about by diffusion so far as movement of the sugar molecule is concerned. The line between adsorption compounds and compounds due to chemical reactions is by no means a sharp one. In fact, it is one of the great battle lines in physical chemistry. One seriously doubts whether anything is gained by his assumption of adsorption compounds. There is much more evidence to support his view that sugar travels from cell to cell mainly by protoplasmic connections rather than by passing through the ectoplast, which is almost impermeable to sugar.—WM. CROCKER.

Physiological diseases.—BONCQUET[19] claims to have solved the mystery of certain plant diseases of the so-called physiological type, such as curly top

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[18] MANGHAM, SYDNEY, On the mechanism of translocation in plant tissues. A hypothesis, with special reference to sugar conduction in sieve tubes. Ann. Botany **31**:293–311. 1917.

[19] BONCQUET, P. A., Presence of nitrites and ammonia in diseased plants. Jour. Amer. Chem. Soc. **38**:2572–2576. 1916.

BONCQUET, P. A., and BONCQUET, MARY, Presence of nitrites and ammonia in diseased plants. II. Oxidases and diastases; their relation to the disturbance. Jour. Amer. Chem. Soc. **39**:2088–2093. 1917.

of sugar beets, curly dwarf of potatoes, mottled leaf of potatoes, and mosaic disease of tobacco. Nitrites and ammonia were detected in the juices extracted from diseased plants. Their origin is supposed to be due to the action of nitrate-reducing bacteria, since the presence of these bacteria in the tissues runs parallel to the presence of nitrites and ammonia. The idea is advanced that the characteristic symptoms in all of these diseases are due to nitrogen starvation. The plants are deprived of nitrates taken up by the roots, because of their bacterial reduction to nitrites and ammonia.

The increase of the oxidases in the tissues of plants affected with some of these diseases has been well established. This biochemical phenomenon is easily incorporated into the author's hypothetical scheme. The results of an exhaustive microchemical study, including a histological method for the detection of oxidases, are said to indicate that the increase of the oxidases in the plants affected with bacterial nitrogen starvation is a direct effort of the physiological functions of the plants to overcome the reducing forces of the bacteria. In making such a statement it must be assumed that the oxidation of phenol derivatives by plant tissues is a measure of their power to oppose nitrate reduction. Experiments are recorded and arguments brought forth to show the increased tendency and effort of the diseased plant to make good the loss of nitrates by bacterial reduction. These arguments are not easily followed, as they seem to be based upon the theory that the absorption of salts by plants is a function of the amount of water taken up by the roots.

The announcement of the apparent ease with which supposed causal organisms have been isolated from tissues of plants affected with this class of disease is rather startling, since several years of persistent effort by a number of workers has hitherto failed to establish definitely the parasitic character of these diseases.—CHAS. O. APPLEMAN.

VOLUME LXV NUMBER 3

THE

BOTANICAL GAZETTE

MARCH 1918

SEXUALITY IN RHIZINA UNDULATA FRIES

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(WITH PLATES III AND IV)

Although in recent years a considerable number of papers have appeared dealing with the phenomena of sexuality in the Ascomycetes, certain of the natural orders in this group have received little attention. In the Discomycetes practically all the species which have been investigated are members of the Pezizales, and few facts are available concerning the sexual process in representatives of any other order. Our knowledge of the morphology of the sexual organs and the behavior of the sex nuclei in the Helvellales is particularly meager. The following brief discussion of the important papers which have been published on the cytology of these fungi will serve to emphasize this fact.

BROWN (11) describes the development of the ascocarp in two species of *Leotia*. In *L. lubrica*, at the base of the youngest fruit-body sectioned, he discovered a large, vacuolated cell having the appearance of an emptied ascogonium. From this cell he found arising a number of hyphae of larger diameter than the other hyphae of the ascocarp. These larger hyphae were empty, and, although they could not be followed for any great distance, they seemed to be connected higher in the fruit-body with the ascogenous hyphae. He apparently found evidences of this ascogonium-like structure in only one specimen, since he states nothing to the contrary, and does not describe other stages in its development. He gives no data

concerning nuclear conditions in this cell nor in the hyphae to which it gives rise, and makes no mention either of the presence or absence of an antheridium. Moreover, in the single other species which he studied, *L. chlorocephala*, he finds no indication of the presence of sexual organs, and states merely that the ascogenous hyphae have their origin in the stipe.

CARRUTHERS (14) discusses in some detail the cytology of *Helvella crispa*, placing particular emphasis on the nuclear divisions in the ascus. He states definitely that sexual organs are absent in this species, and describes apogamous nuclear fusions in undifferentiated hyphae of the hypothecium. Although in the summary of his paper he states that the cells containing the fusion nuclei give rise to the ascogenous hyphae, this important point is not mentioned in the discussion of his results and no figures are given demonstrating it. He states further that "there is evidence that mitoses in the vegetative and ascogenous hyphae show respectively 2 and 4 chromosomes," and says that the third nuclear division in the ascus is brachymeiotic, there being 4 chromosomes in the prophase, while only 2 pass to the poles.

DITTRICH (24) states that in *Mitrula phalloides* the ascogenous hyphae arise near the center of the fruit-body from a complex of closely massed, elongated, deeply staining filaments characterized by the possession of large nuclei with prominent nucleoli. He finds no sexual organs, and does not describe an approximation or fusion of nuclei in the hypothecium.

MCCUBBIN (53) states that in *Helvella elastica* "no structure having the conventional form of an ascogonium" is found, and says that the ascogenous hyphae "arise as a clearly differentiated subhymenial complex of filaments." However, he describes at considerable length large cellular bodies which occur irregularly throughout the whole of the ascocarp except the stem. He regards these as vegetative in function and calls them storage bodies. In the earliest stages in the development of the fruit-body they are absent, but they appear relatively early. They are large, attaining in some cases 20–30 times the diameter of the surrounding hyphae, are filled with deeply staining protoplasm, and exhibit remarkable variation in shape. They sometimes form a chain

of 3 or 4 connected cells. By the time the asci are mature they are usually empty, their connections have disappeared, and their walls have collapsed. McCUBBIN states that these structures in some instances give rise to palisade hyphae and paraphyses, while at other times they are found "having the ascogenous hyphae proceeding directly from them." They contain nuclei varying in number from 1 to 20 or more, a conspicuous feature being the frequent arrangement of these nuclei in pairs. McCUBBIN gives a number of illustrations showing the variation in size and shape of these structures and demonstrating clearly the paired condition of the nuclei. Several significant facts would seem to indicate that at least part of these "storage bodies" constitute some type of sexual apparatus, particularly the statement that they are sometimes found giving rise to the ascogenous hyphae.

FAULL (**26**) discusses the method of origin of the asci from the ascogenous hyphae in a considerable number of species representative of various genera of the Helvellales. He has not investigated the sexual process, however, or described sexual organs in any of the forms studied.

In so far as the writer is aware, no other papers of importance bearing on the sexual process in the Helvellales have appeared. In no member of this group is our knowledge more than fragmentary; in fact it cannot be stated with certainty that any worker has seen the sexual organs in any species of the order. The family Rhizinaceae has received no attention whatever from the standpoint of cytology. As representative of this family, *Rhizina undulata* Fries, is especially suitable for investigation. It is the type of the genus and the family, and probably the most widely distributed and best known member of the group.

Materials and methods

In the summer of 1914 the writer collected a considerable number of apothecia of *Rhizina undulata* in a small pine wood north of Beebe Lake near the Cornell University Campus at Ithaca, New York. Fruit-bodies of practically all stages of development were obtained. The youngest stages, including undifferentiated primordia, were studied, and the results of the investigation were

embodied in an account of the origin of the ascocarp in this species (FITZPATRICK **27**). During the course of this investigation the examination of certain slides disclosed the fact that the material was favorable for a study of the sexual process. Additional slides were then prepared, and material of all ages was given critical examination.

The apothecia were fixed in the field in medium strength chromo-acetic acid fixer, and were later imbedded in paraffin. The material was studied in serial sections 4–7 μ in thickness and was stained in most cases with Haidenhain's iron alum-haematoxylin, although for certain stages the shortened Flemming's triple stain proved more satisfactory.

Certain of the apothecia on which the investigation is based were sectioned and stained in the laboratories of the Brooklyn Botanic Garden in the summer of 1915, while the writer held a visiting fellowship at that institution. He wishes to express here his appreciation of the courtesy of Director C. S. GAGER in extending to him all the facilities of the laboratories and gardens, and to acknowledge his indebtedness to Dr. E. W. OLIVE for many kindnesses, including helpful suggestions concerning microtechnique. Subsequently other apothecia were sectioned and stained in the laboratories of the Department of Plant Pathology at Cornell University. All the critical study of the material was made at the latter institution during the spring of 1916. The writer's identification of the species as *Rhizina undulata* was confirmed independently by Dr. E. J. DURAND and Dr. F. J. SEAVER. The completed manuscript was examined by Professor GEORGE F. ATKINSON. His criticisms, especially with reference to the interpretation of the meaning of the paired condition of the nuclei in the cells of the archicarp, have been embodied in the text, and have resulted in extensive alterations. The writer wishes to express his appreciation of these favors.

Vegetative hyphae

The mycelium of *Rhizina undulata* is parasitic on the roots of various trees (HARTIG **42, 43, 44,** TUBEUF **63,** WEIR **64**). It develops profusely in the soil also, enveloping the soil particles and smaller roots as a whitish, moldlike growth. On the surface of the ground

and on partially exposed roots a definite subiculum is thus produced, upon which minute, snow white knobs of mycelium are developed. These constitute primordia of fruit-bodies. They are composed of undifferentiated hyphae, but a somewhat indefinite palisade layer is formed over the periphery of the primordium. At their initiation, these primordia are extremely minute, averaging approximately 0.3 mm. in lateral diameter. There is no indication other than shape that they are to develop into ascocarps. Sexual cells at this early period are certainly absent. The hyphae composing the primordium are all of approximately the same diameter, and consist of narrow, cylindrical, multinucleate cells. Uninucleate or binucleate cells are not found. These hyphae in many instances can be traced back toward the point of origin of the primordium, where they are either lost in the tangle of hyphae composing the subiculum or are found to enter the soil.

The ascocarp primordium increases in size chiefly by the elongation and branching of the palisade hyphae at the periphery. At the same time the palisade layer becomes more sharply demarcated. The fruit-body, as demonstrated by the writer in his earlier paper, is not, either at the beginning or at any later period, provided with an enveloping membrane. The ascocarp in this species is therefore gymnocarpous, the hymenium being "exposed from the first."

The nuclei in the cells of the vegetative hyphae are small, and were studied with difficulty. A small amount of chromatic material and a deeply staining nucleolus may be seen in each. No division figures have been observed. It is possible that mitosis occurs only at night, all the material having been placed in the fixer at one time during the day. However, the minute size of the nuclei would render any study of nuclear division in the vegetative hyphae extremely difficult. The nuclei occur irregularly throughout the hyphae, and give no indication of pairing or of any other definite arrangement. Deeply staining granules are present in the cytoplasm. These extranuclear bodies, possibly the metachromatic granules of GUILLIERMOND (**35**), are of doubtful function. Sometimes they are found grouped over the opposite faces of the transverse septa. A similar condition exists in *Ascophanus carneus*, where, according to CUTTING (**18**), they guard a minute pore in the

septum. In *R. undulata* no such pores have been demonstrated. Such protoplasmic connections, however, are of frequent occurrence in the fungi. They were first observed by CHMIELEWSKY (15). Subsequently they have been the object of research by DANGEARD (19, 20, 21) in *Sphaerotheca Humuli*, *Bactridium flavum*, and other fungi; and have been studied in various species by MASSEE (52), KIENITZ-GERLOFF (48), MEYER (54), GUILLIERMOND (37), and others. MEYER in particular has given them considerable attention and has demonstrated that open pores exist in the transverse septa of the hyphae of many Basidiomycetes and Ascomycetes. They possibly function in permitting a more rapid transfer of food material from cell to cell.

Archicarp

When the ascocarp primordium has attained a diameter of approximately 1 mm., differentiation begins to take place, certain hyphae lying near its center undergoing transformation into archicarps. The number of archicarps developed in the interior of a single ascocarp varies, and when several archicarps lie closely approximated their interweaving renders an exact count difficult. A careful study, however, of all the consecutive sections of a complete series through the ascocarp demonstrates that the number is in some cases as many as 8, and in many individuals probably more. No ascocarp containing less than 3 archicarps has been found. Although lateral fusion of adjacent apothecia resulting in the formation of irregular compound structures is a common phenomenon, it fails to explain the presence of more than a single archicarp in a fruit-body. Ascocarps of circular form which are clearly the result of the enlargement of a single primordium contain several archicarps. Moreover, young primordia in which lateral fusions have certainly not taken place reveal several archicarps in the process of development.

While the production of several archicarps in a single apothecium is unusual in the Discomycetes, this condition being more typical of the discomycetous lichens, it is not unique. OVERTON (56) finds that in *Thecotheus Pelletieri* the apothecium is compound, the fruit-body arising from several multicellular archicarps. In other Discomycetes, of which *Pyronema confluens* is perhaps the

best known example, several pairs of ascogonia and antheridia contribute to the formation of a single apothecium. In the majority of the Discomycetes which have been studied, however, a single archicarp is developed. Of these may be enumerated *Lachnea scutellata* (BROWN 12, WORONIN 69), *Peziza granulosa* and *Ascobolus pulcherrimus* (WORONIN 69), *Ascobolus furfuraceus* (JANCZEWSKI 45, 46, HARPER 39, WELSFORD 65), *Ascodesmis nigricans* (VAN TIEGHEM 61), *Ryparobius* sp. (BARKER 4, 5), *Thelebolus stercoreus* (RAMLOW 57), *Lachnea scutellata* (BROWN 12), *Humaria granulata* (BLACKMAN and FRASER 9), *Ascophanus carneus* (CUTTING 18), and *Lachnea cretea* (FRASER 30). As representative of lichens containing several archicarps in a single apothecium may be listed *Parmelia acetabulum* (BAUR 7, 8), *Anaptychia ciliaris*, *Lecanora subfusca*, *Endocarpon miniatum*, *Gyrophora cylindrica*, and *Cladonia pyxidata* (BAUR 8), *Pertusaria communis* and *Pyrenula nitida* (BAUR 7), and several species of *Collema* (BAUR 6, BACHMANN 2, 3).

The individual archicarp of *R. undulata* arises by the rapid growth and transformation of a single multicellular hypha. The cells increase greatly in lateral diameter and become filled with deeply staining protoplasm, so that the resulting structure assumes a dense and opaque appearance. The relatively few nuclei originally present undergo repeated division, and each cell of the archicarp is soon packed with many nuclei. The cells of the archicarp are certainly multinucleate from the first. In *Ascobolus*, according to HARPER (39) and WELSFORD (65), the cells of the archicarp are uninucleate at the beginning, while in other forms (BROWN 12 *Lachnea scutellata*, CUTTING 18 *Ascophanus carneus*) they are described as multinucleate in all stages.

The diameter of the cells of the archicarp when the ultimate size is reached is much greater than that of the surrounding hyphae, and for this reason no possibility exists of mistaking an archicarp for an ordinary hypha, even when the lower powers of the microscope are used. This difference in size is strikingly shown in fig. 4. Cells of a mature archicarp sometimes measure 10 times the diameter of the other hyphae.

The archicarp is in all cases multicellular, the number of cells varying in the counts made from 10 to 19. Different individuals

have been followed carefully from base to apex throughout the various sections of a series, and the cells are found to differ to a marked degree in size and shape. Great variability is also shown in the general form of the archicarp (figs. 1–4). It develops in some cases as a loose coil (fig. 3), in others winds irregularly among the other hyphae (fig. 1), or more rarely bends back upon itself, forming two nearly parallel rows of cells (fig. 4). Irregularly winding archicarps are the most common type. Closely wound coils have not been found. Antheridia are not produced, and no fusion of the terminal cell of the archicarp with any other structure has been observed. Many sections have been examined in vain in an endeavor to demonstrate such fusions. The writer is convinced that none occur.

The terminal cell of the archicarp is smaller than the other cells of this structure. It is usually narrow and attenuated, and at the maturity of the archicarp shows disorganized, deeply staining, protoplasmic contents. It resembles very closely the cell figured and described by CUTTING (**18**) as a trichogyne in *Ascophanus carneus*, and from analogy the writer will refer to it as the trichogyne. It certainly does not function, however, and is evidently merely a vestigial structure.

The archicarp in *R. undulata* is not, as in certain other species, sharply divided into definite apical, central, and basal portions. The cells which give rise to ascogenous hyphae are usually centrally located in the coil, and in some individuals are slightly larger than the other cells, but this is not always the case. No well defined ascogonium is differentiated.

In the younger stages in the development of the archicarp no pores can be detected in the transverse septa. If any exist, they are very minute. Deeply staining, extranuclear granules, resembling those in the vegetative hyphae, are frequently found grouped on opposite sides of the cross walls. Their occurrence is not constant and their function is unknown. Similar granules are also described as occurring in *Ascobolus* (HARPER **39**, WELSFORD **65**), *Ascophanus carneus* (CUTTING **18**), *Pyronema confluens* (HARPER **40**), *Humaria granulata* (BLACKMAN and FRASER **9**), and other Ascomycetes.

As the archicarp of *R. undulata* approaches maturity a very prominent, deeply staining, hemispherical or convex pad appears on each side of each cross wall at or near its center. Similar pads have been found in *Humaria granulata* (BLACKMAN and FRASER **9**), *Ascophanus carneus* (CUTTING **18**), and other forms, but in no case have the figures presented by the investigator shown such striking and definite structures as those in *R. undulata*. Since at a some-what later period a single large pore appears in each of the transverse septa at the point earlier occupied by the pads, it seems probable that the latter represent a swelling out of the septum due to gelatinization at this point. CUTTING has suggested that the metachromatic granules mentioned may function in bringing about such a gelatinization. It is certain, in any case, that the pads are absent in young archicarps; that with the approach of maturity they are prominent; and that still later they disappear, leaving behind a well defined pore in the septum. CUTTING found pads in *Ascophanus carneus* lying free in the cytoplasm of the archicarp following the appearance of the pores. Attached to these he observed what seemed to be bits of the wall on which they originally lay. The writer, however, has not seen any such detached pads in *R. undulata*.

Near the apex of the archicarp shown in fig. 3 may be seen the union of the two pads which originally lay separated on the opposite faces of the septum. We may assume that this fusion represents the last stage in gelatinization. CUTTING (**18**) figures a similar condition (his fig. 14) in an archicarp of *Ascophanus carneus*.

Although the disappearance of these pads takes place suddenly, the process does not occur simultaneously on all the transverse septa. In fact, neither in the development of the pads nor in their removal is any definite sequence followed as regards the relative position of the septa in the archicarp. In the youngest archicarp shown (fig. 1) not all of the pads have been formed. In an older archicarp (fig. 4) all have disappeared, leaving definite open protoplasmic connections. In intermediate stages (figs. 2, 3) some pads have disappeared while others remain.[1] Rarely a single pair of pads persists on a septum until the formation of ascogenous hyphae has

[1] Read the introductory paragraph in the explanation of plates.

progressed to a marked degree (fig. 7). The mature archicarp, on account of its very dense protoplasmic contents and numerous nuclei, stains very deeply, and in many cases is practically opaque. Not all the individuals stained prove favorable, therefore, for the demonstration of protoplasmic continuity. Moreover, on account of the winding course of the archicarp, which results in the appearance of different portions of a single coil in several different sections, not all of the pores or pads are visible in the plane of one section. When the position of the archicarp is favorable careful staining renders the pores very evident (figs. 4, 7). They are slightly greater in diameter than a single nucleus. The ascogenous hyphae in some cases (figs. 3, 7) arise before all of the pads have disappeared; in other cases (fig. 4) all of the pores may be formed before any indication of the development of ascogenous hyphae is given.

Ascogenous hyphae

As stated earlier, no definite group of cells in the archicarp gives rise to the ascogenous hyphae. Usually 4 or 5 consecutive cells lying near the center of the coil function as ascogonial cells. These put out a considerable number of ascogenous hyphae, which by repeated branching develop a large number of free ends for the formation of ascus hooks. The other cells of the archicarp meantime fail to bud, and their nuclei and cytoplasm flow through the open connections in the transverse septa into the active ascogonial cells and thence into the ascogenous hyphae. All the cells of both the apical (exclusive of the trichogyne) and basal regions contribute their contents to this general flow, and are finally almost entirely emptied. This migration is shown clearly in figs. 5 and 6. Figs. 8, 9, 10, and 11 represent at a considerably higher magnification sections through ascogonial cells at right angles to the long axis of the archicarp. In two of these (figs. 10, 11) the ascogenous hyphae are shown at their point of origin from the archicarp. The others (figs. 8, 9) represent sections through budding cells at points between the places where hyphae arise. A pronounced vacuolation of the cytoplasm of the ascogonial cells occurs at the time of the outward flow of nuclei into the ascogenous hyphae. Since the vacuolation is more evident in the center of the cell, the nuclei

which remain behind lie at this stage in a rather restricted zone at the periphery.

This pronounced vacuolation and thinning of the cytoplasm of the ascogonial cells renders less difficult the study of the nuclei, and at this stage, in the writer's preparations, they seem always to lie in pairs. At no other stage in the development of the archicarp, either before or after the formation of pores in the transverse septa, have paired nuclei been found in any of the cells of this structure. This, however, may be due in large measure to the fact that the dense nature of the cytoplasm and the crowding of the nuclei render the determination of this point extremely difficult.

The presence of paired nuclei in any of the cells of the archicarp is a matter of the greatest interest and importance. This is especially true since an antheridium is absent. The determination of the origin of the two nuclei which constitute a pair, however, is fraught with considerable difficulty. It is evident that they are either potential sex nuclei which have had their respective origins in the same or different cells of the archicarp, or sister nuclei which have resulted from a recent more or less simultaneous division of the archicarp nuclei. If they are sex nuclei, it is to be expected that they will either fuse in the archicarp or migrate side by side into the ascogenous hyphae, where they will undergo conjugate divisions preceding the fusion in the ascus.

Fusion of these pairs of nuclei in the cells of the archicarp has not been observed. Although occasionally the two nuclei lie in actual contact, fusion stages have not been found. Moreover, no nuclei of larger size have been seen which might from analogy be assumed to be fusion nuclei. A thorough examination of the nuclei in the ascogenous hyphae has failed, moreover, to demonstrate conjugate divisions. In some instances groups of nuclei in fours have been found lying in such a position as to suggest their origin from conjugate divisions, but these cases are not numerous enough to carry conviction. No mitotic figures, either of simple or conjugate division, have been seen in these hyphae, nor in any of the cells of the archicarp. The writer has attributed their absence to the fact that all of his material was placed in the fixing solution at one time. Periodicity of mitosis thus could easily explain their

absence in all of the preparations. Since *R. undulata* is an uncommon species, it is infrequently collected, and the writer, desirous of supplementing his material with preparations showing mitosis, searched for the fungus without success throughout the summers of 1915 and 1916. While unwilling to state that conjugate divisions do not take place in the ascogenous hyphae of this species, he has been unable to demonstrate their occurrence. On the other hand, a periodicity in mitosis which would constitute a more or less simultaneous division of all the nuclei in the archicarp might easily give at the rounding up of the daughter nuclei a marked appearance of pairing. The pairs of nuclei in the ascogenous hyphae could also originate in the same manner. Until mitotic figures, either of simple or conjugate divisions, have been demonstrated in the ascogenous hyphae, it will be well to reserve judgment as to the meaning of the paired condition.

A comparison of our work on *R. undulata* with that of other investigators who have studied the origin of the paired condition in those Ascomycetes in which a male organ is lacking or non-functional is not enlightening. Although great variation exists in their accounts, fusion of nuclei in pairs in the ascogonial cells is described as occurring in *Lachnea cretea* (FRASER 30), *Ascophanus carneus* (CUTTING 18), and *Thecotheus Pelletieri* (OVERTON 56). Conjugate divisions have not been described in any case. CLAUSSEN (17) alone in *Pyronema confluens* has figured conjugate divisions in the undifferentiated portions of the ascogenous hyphae of the Discomycetes.

The ascogenous hyphae of *R. undulata* undergo repeated branching as they approach the hymenium. They soon become multiseptate (fig. 12), the individual cells containing a varying number of nuclei which are usually, though not constantly, in evident pairs. On the transverse septa are found deeply staining granules resembling those in the vegetative hyphae. In some cases these are aggregated into large granules similar to the deeply staining pads of the archicarp, but they are in reality much smaller. Other granules occur throughout the cytoplasm. No open pores in the septa have been demonstrated, and although it is possible that minute protoplasmic connections exist, there is no reason to think that nuclei migrate from cell to cell. In later stages the deeper lying

cells of the ascogenous hyphae become vacuolated, stain lightly, and apparently take no direct part in the formation of the hymenium.

The layer of paraphyses is developed early in the history of the fruit-body and constitutes a well defined zone long before the young asci are developed. This zone is in reality merely a differentiation of the palisade layer of peripheral vegetative hyphae, and its elements have no direct organic connection with the archicarp or ascogenous hyphae.

Early in the history of the archicarp there are developed also paraphysis-like structures, termed setae, which originate far below the hymenium from vegetative hyphae, traverse the hymenium, and protrude beyond it as thick-walled, dark-colored spines. These spines are non-septate tubes which discharge at their tips a brown, glutinous secretion over the surface of the hymenium.

The terminal branches of the ascogenous hyphae push up to the base of the paraphysis layer, and there undergo typical crozier formation. The terminal portions of the hyphae are of smaller diameter than the cells nearer the archicarp. The tip of each branch contains two nuclei, and in some cases these are cut off from the remainder of the thread by a septum. The nuclear membrane is sharply defined and the nucleolus stains deeply. The two nuclei are in some cases closely approximated or actually in contact, while in others they lie relatively remote from each other. The tip of each branch of the ascogenous hyphae forms a single definite hook (figs. 14–21). Although irregular hooks (figs. 17, 18) are not infrequent, complex systems of hooks such as those described by CLAUSSEN (**17**) in *Pyronema confluens*, by BROWN (**11, 12**) in *Leotia*, *Lachnea*, and *Geoglossum*, and by MCCUBBIN (**53**) in *Helvella elastica* have not been found.

The two nuclei in the tip of the hypha at the time of crozier formation probably undergo conjugate division in the usual manner. Four nuclei (figs. 19–21) thus result. These drift apart, the uppermost pair passing into the bend of the hook, which then undergoes renewed growth and develops a prominent "dome cell" (fig. 21). The other pair of nuclei come to lie in such a position that one occupies the recurved tip of the hypha and the other the main body of the thread. The two septa frequently figured in

other Ascomycetes are then laid down, and the dome cell thus cut off develops into the ascus.

Ascus

The young ascus increases rapidly in size, and pushes upward among the paraphyses. It assumes a definite cylindrical shape, and its two nuclei, now closely approximated at its center, soon fuse (fig. 23). Fusion nuclei containing two nucleoli are frequently found (figs. 22, 23). After fusion the nucleus increases in size as the ascus enlarges. The two nucleoli evidently fuse, the fusion nucleolus being larger and staining deeply.

The chromatic material undergoes certain changes which call for special comment. The extrusion of chromatic bodies from the nucleus during synapsis or at early stages in meiosis is described by DIGBY (**23**) in *Galtonia candicans*, and by CARRUTHERS (**14**) in *Helvella crispa*. They state that these bodies may arise either from the nucleolus or nuclear framework. In both cases they are impregnated with chromatin. They are ejected forcibly through the nuclear membrane, and on escaping become definitely pyriform by constriction. They are sometimes drawn out behind into a fine thread and by means of this remain attached to the nucleus for a considerable time. Figures of these bodies given by CARRUTHERS resemble very closely similar bodies present in *R. undulata*. A comparison of the figures presented in the two cases shows them to be strikingly similar. However, the writer is unprepared to state that in *R. undulata* they actually represent ejected chromatin. It is certain that bodies taking the stain in a similar manner may be found in the cytoplasm of the ascus remote from the nucleus (figs. 22, 24, 27).

The mature ascus of *R. undulata* contains 8 unicellular hyaline spores. No attempt has been made to study the method of cutting out of the spores, nor has any critical examination been given to the nuclear divisions in the ascus.

General considerations

It is not necessary to review here the history of the development of our knowledge of the sexuality of the Ascomycetes. This task has been thoroughly accomplished by other workers. The earlier

papers bearing upon the subject are excellently reviewed by HARPER (**40, 41**), LOTSY (**50**), OVERTON (**56**), and GUILLIERMOND (**37**); while more recent literature has been discussed by FRASER (**29**), RAMSBOTTOM (**58, 59**), DODGE (**25**), and ATKINSON (**1**). It will prove profitable, however, to call attention to the more important general problems which are encountered in the investigation of the sexual phenomena in this group, and to review briefly the results of certain researches which bear directly upon our own study of *Rhizina undulata*.

The great difference of opinion which exists in the interpretation of the nuclear phenomena in the ascogonium, ascogenous hyphae, and asci has resulted in general uncertainty as to the real essence of sexuality in the Ascomycetes. Certain investigators maintain that the fusion nucleus of the ascus is the product of two successive nuclear fusions, the first of these taking place usually in the archicarp and constituting the sexual fusion, while the second occurs in the young ascus and is regarded as vegetative. HARPER (**41**) explains the occurrence of this second fusion in the ascus as an attempt on the part of the fungus to maintain the nucleocytoplasmic relation or equilibrium in the cell, a large cell such as the ascus requiring a large nucleus (DANGEARD **19**, HARPER **38**, WINGE **67**). He states further that his researches indicate "that the fusion of the nuclei in the young ascus does not result in doubling the number of chromosomes as they appear in the succeeding divisions." Other investigators of this group, however, maintain that the fusion nucleus of the ascus is as the result of the two fusions necessarily tetraploid, and undergoes during the progress of the three divisions in the ascus a double reduction, the haploid number of univalent chromosomes being reached in each of the 8 resulting nuclei. FRASER (**28** *Humaria rutilans*) and others (FRASER and BROOKS **31** *Humaria granulata*, *Ascobolus furfuraceus*, *Lachnea stercorea*, FRASER and WELSFORD **32** *Otidea aurantia*, *Peziza vesiculosa*, and CARRUTHERS **14** *Helvella crispa*) state also that the third division in the ascus accomplishes the second reduction by a unique process termed brachymeiosis. In the later stages of this mitosis, according to their accounts, whole chromosomes are pulled toward the poles, the number in the telophase thus being reduced to one-half that in the prophase.

Many other investigators, however, maintain that the nuclear fusion in the ascus constitutes the only fusion in the life cycle, and state that the third division in the ascus is a typical vegetative mitosis. FAULL (**26** *Hydnobolites*, *Neotiella*) and CLAUSSEN (**17** *Pyronema confluens*) state that the same number of chromosomes is found in each of the three divisions in the ascus, and HARPER (**40** *Pyronema confluens*, **41** *Phyllactinia Corylea*), who describes a double fusion, also finds the chromosome number remaining constant.

Although many Ascomycetes have been examined in the endeavor to reach a satisfactory solution of the questions involved in this controversy, investigators are now as far as ever from agreement. The minute size of the sexual nuclei and the consequent difficulty encountered in demonstrating fusion renders misinterpretation easy. It is possible, as suggested by BROWN (**12**), that nuclear division in the ascogonium has been mistaken for fusion. Moreover, the presence of V-shaped chromosomes in the third division in the ascus in some species at least probably explains the differences in chromosome counts made by different investigators. It is possible also that coalescence of degenerating nuclei has been mistaken for a sexual fusion.

It will be admitted also that two lines of a priori argument have contributed to the general disagreement concerning the essential facts in the nuclear history of the Ascomycetes. One group of investigators maintains that two successive nuclear fusions in a single life cycle, resulting in the production of a fusion nucleus with the $4x$ chromosome number, followed by a double reduction embracing the remarkable process of brachymeiosis, constitute a phenomenon so unusual as to warrant skepticism and to demand absolute proof. Since no similar variation has been found in any other group of organisms they doubt its occurrence in the Ascomycetes.

The other school of workers lay great stress upon the presence of 8 spores in the ascus of so many Ascomycetes, and point out that even in asci containing fewer spores than 8 the production of 8 nuclei as the result of the triple division of the fusion nucleus has been described in practically every species investigated. This almost universal occurrence of the triple division in the ascus is ascribed

by them as due to the "quadrivalent character" of the chromosomes in the fusion nucleus, which renders 3 mitoses necessary for the return to the univalent condition. When fewer than 8 spores are formed, the supernumerary nuclei degenerate (HARPER **41** *Phyllactinia Corylea*) or two or more nuclei are incorporated in one spore (WOLF **68** *Podospora anserina*). When many-spored asci are formed, additional vegetative nuclear divisions take place following the triple division.

In *Eremascus fertilis* (STOPPEL **60,** GUILLIERMOND **36**) the triple division occurs, but, as ATKINSON (**1**) has pointed out, there is here certainly only a single fusion, the antheridium and ascogonium being uninucleate and the fertilized ascogonium functioning as the ascus after fusion has occurred. Also in *Dipodascus albidus* (JUEL **47**) and *Endomyces Magnusii* (GUILLIERMOND **36**) essentially the same process takes place; a single nuclear fusion precedes spore formation, and the fertilized ascogonium functions directly as the ascus. In *Endomyces Magnusii*, moreover, according to GUILLIERMOND, only two divisions occur in the ascus and 4 uninucleate spores are formed.

The triple division in the ascus resembles very closely the process in the Basidiomycetes by which the basidium in some species (FRIES **33** *Nidularia pisiformis*, LEVINE **49** *Boletus* spp., *Strobilomyces strobilaceus*) produces as the result of 3 successive nuclear divisions 8 nuclei, which appear in 4 binucleate spores. Since in these cases the 3 divisions follow one another rapidly and a rest period then ensues, the resemblance to the process in the Ascomycetes is marked. LEVINE describes the third division as taking place always in the spore, and states that in *Boletus albellus* a fourth division occurs, the resulting 4 spores being tetranucleate. FRIES states that in *Nidularia pisiformis* uninucleate spores are never found, and says that immediately upon the entrance of the nucleus completely into the spore a spindle is seen forming. He believes that the nucleus while migrating through the canal of the sterigma is already in the prophase of division. When it reaches the spore the equatorial plate is formed at once. MAIRE (**51**) in *Clavaria rugosa* and *Cantharellus cinereus* figures the third division as taking place in the basidium itself.

The questions involved in the study of the nuclear history of the Ascomycetes will never be satisfactorily answered by a priori argument. The careful examination of a large number of representatives of this group presenting peculiarly favorable material for investigation, and the comparison of the data obtained with those available for other groups will, however, go far toward explaining the discrepancies in conflicting accounts and toward answering vexing questions to the satisfaction of all students.

The greatest variation is evident in the morphology of the sexual apparatus in the Ascomycetes even in forms in which the gross structural characters of the ascocarp are very similar. The published evidence would seem to show, moreover, that a certain amount of variation in the unfolding of the sexual phenomena may be encountered in the investigation of even a single species.

In *Pyronema confluens* the sexual phenomena have been variously described. HARPER (**40**) gives in detail the passage of the male nuclei from the antheridium into the ascogonium, their fusion there in pairs with the female nuclei, the migration of the fusion nuclei into the ascogenous hyphae, and later a second fusion in the ascus. CLAUSSEN (**16, 17**) also describes the entrance of the antheridial nuclei into the ascogonium, but states that they merely pair there with the female nuclei without fusion. These pairs of nuclei then migrate into the ascogenous hyphae where they divide conjugately, two nuclei ultimately fusing in the ascus to give a fusion nucleus with the diploid number of chromosomes. This demonstration by CLAUSSEN of conjugate divisions in the ascogenous hyphae is especially noteworthy, since these divisions in the undifferentiated portions of the hyphae have not been demonstrated elsewhere in the Discomycetes. Since these nuclei divide conjugately, there is good reason to feel that they are linked together by a sexual attraction. FRASER (**30**), however, says that "the phenomenon of conjugate division is probably but a special example of the very general fact that nuclei present in the same cell usually divide simultaneously" (FROMME **34**, OLIVE **55**). WELSFORD (**66**) suggests that the paired condition of the nuclei may be merely the response to the physiological conditions usually found in rapidly developing hyphae. VAN TIEGHEM (**62**) grew under cultural con-

ditions a form which he stated to be *Pyronema confluens* and was able to develop normal or rudimentary antheridia or to suppress them entirely, while the ascogonia developed normally under all conditions. DANGEARD (**22**) found in what he regarded as the same species that even in cases in which the antheridium fuses with the trichogyne the male nuclei degenerate *in situ*, and fail to enter the ascogonium. BROWN (**10, 13**), working with a strain which he has named *Pyronema confluens* var. *inigneum*, found that the ascogonia and antheridia fail to fuse, and states that only one nuclear fusion, that in the ascus, occurs in the life cycle. He also examined the parent species, and states that in it he found migration of male nuclei into the ascogonium. *Pyronema confluens* var. *inigneum*, according to the account of BROWN, differs from the parent species physiologically also in that it grows freely upon an unsterilized substratum. The variation in the accounts of the different workers who have examined this species would seem to show that in this form the degeneration of the antheridium is now taking place. On account of the small size of the nuclei the demonstration of fusion in the ascogonium, however, is extremely difficult and it is possible that two investigators might reach a different conclusion from the examination of a single set of slides.

The writer feels that neither in *Pyronema confluens* nor in any other Ascomycete have two successive nuclear fusions in a single life cycle been conclusively demonstrated. It is evident that we cannot depend upon a critical examination of the nuclear divisions in the ascus to tell whether or not one or two fusions have occurred, since here also a fundamental difference in interpretation exists. Although FRASER and her co-workers figure and describe brachymeiosis in several species, HARPER and others find the chromosome number remaining constant throughout the three divisions in the ascus.

Summary

1. The sexual process has not heretofore been studied in any member of the Rhizinaceae. The examination of *Rhizina undulata* Fries is therefore of considerable interest.

2. Material for study was collected at Ithaca, New York, and a paper describing the origin of the apothecium in this species has already been published (**27**).

3. The vegetative mycelium is parasitic on the roots of trees, and develops profusely in the soil. On the surface of the ground or on parasitized roots minute primordia of fruit-bodies are developed. These are composed of undifferentiated hyphae which form at the periphery a somewhat indefinite palisade layer.

4. After the ascocarp primordium has attained a diameter of approximately 1 mm., certain hyphae near its center are transformed into archicarps. As many as 8 archicarps may be developed in a single ascocarp.

5. The individual archicarp develops by the rapid growth and transformation of an ordinary multicellular hypha. Its cells are multinucleate from the first. The nuclei increase greatly in number by repeated division and the archicarp soon takes on a dense opaque appearance.

6. An antheridium is absent.

7. The archicarp develops in some cases as a loose coil, and in others winds irregularly among the other hyphae, but tight coils have not been found. The number of cells in a single archicarp has been found to vary from 10 to 19 or more.

8. The terminal cell of the archicarp is small and attenuated, and at maturity shows disorganized protoplasmic contents. It has been here from analogy termed the trichogyne, but it certainly does not function.

9. As the archicarp approaches maturity a single, very prominent, deeply staining, hemispherical or convex pad appears on each side of the transverse septa. These pairs of deeply staining pads apparently represent a swelling of the wall due to gelatinization at that point. They later fuse and finally disappear, leaving a large pore in the septum.

10. Approximately one-half of the cells of the archicarp lying at the center of the coil now put out ascogenous hyphae. The remaining basal and apical cells fail to bud, and their nuclei and cytoplasm flow through the pores in the transverse septa into the ascogonial cells, and thence into the ascogenous hyphae.

11. With the outward flow of nuclei and cytoplasm into the ascogenous hyphae, the cytoplasm in the ascogonial cells of the archicarp becomes pronouncedly vacuolated. The nuclei are then seen to lie in pairs. In preceding stages the dense nature of the protoplasm and the crowding of the nuclei render the demonstration of a paired condition extremely difficult. Pairs of nuclei in the archicarp have been seen only in cells giving rise to ascogenous hyphae.

12. Careful search has failed to demonstrate stages of nuclear fusion in the ascogonial cells or in the ascogenous hyphae.

13. Paired nuclei are also present in the ascogenous hyphae. Neither conjugate nor simple divisions have been demonstrated.

14. Crozier formation takes place, but elaborate systems of hooks at the ends of the ascogenous hyphae have not been found. Nuclear fusion occurs in the young ascus.

DEPARTMENT OF PLANT PATHOLOGY
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LITERATURE CITED

1. ATKINSON, G. F., Phylogeny and relationships in the Ascomycetes. Ann. Mo. Bot. Gard. **2**:315–376. *figs. 10.* 1915.
2. BACHMANN, FREDA M., A new type of spermagonium and fertilization in *Collema*. Ann. Botany **26**:147–760. 1912.
3. ———, The origin and development of the apothecium in *Collema pulposum* (Bernh.) Ach. Archiv Zellforschung **10**:369–430. *pls. 30–36.* 1913.
4. BARKER, P. T. B., The development of the ascocarp in *Ryparobius*. Rep. British A.A.S. Southport. 849–850. 1903.
5. ———, Further observations on the ascocarp in *Ryparobius*. Rep. British A.A.S. Cambridge. 825–826. 1904.
6. BAUR, E., Zur Frage nach der Sexualität der Collemaceen. Ber. Deutsch. Bot. Gesells. **16**:363–367. 1898.
7. ———, Die Anlage und Entwicklung einiger Flechtenapothecien. Flora **88**:319–332. *pls. 14, 15.* 1901.
8. ———, Untersuchungen über die Entwickelungsgeschichte der Flechtenapothecien I. Bot. Zeit. **62**:21–44. *pls. 1, 2.* 1904.
9. BLACKMAN, V. H., and FRASER, H. C. I., On the sexuality and development of the ascocarp of *Humaria granulata* Quel. Proc. Roy. Soc. Lond. Bot. **77**:354–368. *pls. 13–15.* 1906.
10. BROWN, W. H., Nuclear phenomena in *Pyronema confluens*. Preliminary note. Johns Hopkins Univ. Circ. **28**:712–715. 1909.

11. ———, The development of the ascocarp of *Leotia*. BOT. GAZ. **50**:443–459. *figs. 47*. 1910.
12. ———, The development of the ascocarp of *Lachnea scutellata*. BOT. GAZ. **52**:273–305. *pl. 9. figs. 51*. 1911.
13. ———, The development of *Pyronema confluens* var. *inigneum*. Amer. Jour. Bot. **2**:289–298. 1915.
14. CARRUTHERS, D., Contributions to the cytology of *Helvella crispa* Fries. Ann. Botany **25**:243–252. *pls. 18, 19*. 1911.
15. CHMIELEWSKY, W., Zur Morphologie des *Haplotrichum roseum* Corda. Memoiren der Neurussichen Naturforscher-Gesellschaft. **11**:23–38. *pl. 1*. 1886 (Russisch); see JUST'S Botanisches Jahresbericht **16**:299. 1888.
16. CLAUSSEN, P., Zur Kenntnis der Kernverhältnisse von *Pyronema confluens*. Ber. Deutsch. Bot. Gesells. **25**:586–590. 1907.
17. ———, Zur Entwickelungsgeschichte der Ascomyceten. *Pyronema confluens*. Zeitschr. Bot. **4**:1–64. *pls. 1–6. figs. 10*. 1912.
18. CUTTING, E. M., On the sexuality and development of the ascocarp in *Ascophanus carneus* Pers. Ann. Botany **23**:399–417. *pl. 28*. 1909.
19. DANGEARD, P. A., La reproduction sexuelle dans le *Sphaerotheca Castagnei*. Le Botaniste **5**:27–31. 1896.
20. ———, Seconde memoire sur la reproduction sexuelle des Ascomycetes. Le Botaniste **5**:245–284. 1897.
21. ———, Structure et communication protoplasmiques dans le *Bactridium flavum*. Le Botaniste **7**:33–45. 1900.
22. ———, Recherches sur le développement du périthece chez les Ascomycetes. Le Botaniste **10**:1–385. *pls. 1–91*. 1907.
23. DIGBY, L., Observations on "chromatin bodies" and their relation to the nucleolus in *Galtonia candicans* Decsne. Ann. Botany **23**:491–502. *pls. 33, 34*. 1909.
24. DITTRICH, G., Zur Entwickelungsgeschichte der Helvellineen. Cohn's Beiträge zur Biologie der Pflanzen. **8**:17–52. *pls. 4, 5*. 1898.
25. DODGE, B. O., The morphological relationships of the Florideae and the Ascomycetes. Bull. Torr. Bot. Club **41**:157–202. *figs. 13*. 1914.
26. FAULL, J. H., Development of ascus and spore formation in Ascomycetes. Proc. Bost. Soc. Nat. Hist. **32**:77–114. *pls. 7–11*. 1905.
27. FITZPATRICK, H. M., The development of the ascocarp of *Rhizina undulata* Fr. BOT. GAZ. **63**:282–296. *pls. 17, 18*. 1917.
28. FRASER, H. C. I., Contributions to the cytology of *Humaria rutilans* Fries. Ann. Botany **22**:35–55. *pls. 4, 5*. 1908.
29. ———, Recent work on the reproduction of Ascomycetes. Trans. Brit. Mycol. Soc. **3**:100–107. 1909.
30. ———, The development of the ascocarp in *Lachnea cretea*. Ann. Botany **27**:553–563. *pls. 42, 43*. 1913.
31. FRASER, H. C. I., and BROOKS, W. E. ST. JOHN, Further studies on the cytology of the ascus. Ann. Botany **23**:537–549. *pls. 34–40. fig. 1*. 1909.

32. FRASER, H. C. I., and WELSFORD, E. J., Further contributions to the cytology of the Ascomycetes. Ann. Botany **22**:465–477. *pls. 26, 27.* 1908.
33. FRIES, R., Über die cytologischen Verhältnisse bei der Sporenbildung von *Nidularia*. Zeits. Bot. **3**:145–165. 1911.
34. FROMME, D., Sexual fusions and spore development of the flax rust. Bull. Torr. Bot. Club **39**:113–131. *pls. 8, 9.* 1912.
35. GUILLIERMOND, A., Contribution à l'étude de l'épiplasme des Ascomycètes et recherches sur les corpuscules métachromatiques des Champignons. Ann. Mycol. **1**:201–215. *pls. 6, 7.* 1903.
36. ———, Recherches cytologiques et taxonomiques sur les Endomycetées. Rev. Gen. Bot. **21**:354–391, 401–419. *pls. 13–19.* 1909.
37. ———, Les progrès de la cytologie des Champignons. Progressus Rei Botanicae **4**:389–542. 1913.
38. HARPER, R. A., Die Entwickelung des Perithecium *Sphaerotheca Castagnei*. Ber. Deutsch. Bot. Gesells. **13**:475–481. *pl. 89.* 1895.
39. ———, Über das Verhalten der Kerne bei der Fruchtentwickelung einiger Ascomyceten. Jahrb. Wiss. Bot. **29**:655–685. *pls. 11, 12.* 1896.
40. ———, Sexual reproduction in *Pyronema confluens* and the morphology of the ascocarp. Ann. Botany **14**:321–400. *pls. 19–21.* 1900.
41. ———, Sexual reproduction and the organization of the nucleus in certain mildews. Carnegie Inst. Washington Publ. **37**:1–104. *pls. 1–7.* 1905.
42. HARTIG, R., Untersuchungen über *Rhizina undulata*. Bot. Centralbl. **45**:237–238. 1891.
43. ———, *Rhizina undulata* Fr. Der Wurzelschwamm. Forst. Naturw. Zeitschr. **1**:291–297. 1892.
44. ———, Textbook of the diseases of trees. Transl. by W. SOMERVILLE, rev. and edit. by H. MARSHALL WARD. 123–129. *figs. 61–70.* 1894.
45. JANCZEWSKI, E., Morphologische Untersuchungen über *Ascobolus furfuraceus*. Bot. Zeit. **29**:257–262, 271–278. *pl. 4.* 1871.
46. ———, Recherches morphologiques sur *l'Ascobolus furfuraceus*. Ann. Sci. Nat. Bot. V. **15**:197–214. 1872.
47. JUEL, H. O., Über Zellinhalt, Befruchtung und Sporenbildung bei *Dipodascus*. Flora **91**:47–55. *pls. 7, 8.* 1902.
48. KIENITZ-GERLOFF, F., Neue Studien über Plasmodesmen. Ber. Deutsch. Bot. Gesells. **20**:93. 1902.
49. LEVINE, M., Studies in the cytology of the Hymenomycetes, especially the Boleti. Bull. Torr. Bot. Club **40**:137–181. *pls. 4–8.* 1913.
50. LOTSY, J. P., Vortrage über botanische Stammesgeschichte **1**:1–828. 1907.
51. MAIRE, R., Recherches cytologiques et taxonomiques sur les Basidiomycètes. Bull. Soc. Mycol. France **18**:1–209. *pls. 1–8.* 1902.
52. MASSEE, G., On *Trichosphaeria Sacchari* Mass. Ann. Botany **7**:515–532. 1893.
53. MCCUBBIN, W. A., Development of the Helvellineae, I. *Helvella elastica*. BOT. GAZ. **49**:195–206. *pls. 14–16.* 1910.

54. MEYER, A., Die Plasmaverbindungen und die Fusionen der Pilze der Florideenreihe. Bot. Zeit. **60**:139–178. *pl. 6.* 1902.
55. OLIVE, E. W., The relationships of the Aecidium-cup type of rust. Science, N.S., **27**:214–215. 1908.
56. OVERTON, J. B., The morphology of the ascocarp and spore formation in the many-spored asci of *Thecotheus Pelletieri*. BOT. GAZ. **42**:450–492. *pls. 29, 30.* 1906.
57. RAMLOW, G., Zur Entwickelungsgeschichte von *Thelebolus stercoreus* Tode. Bot. Zeit. **64**:85–99. 1906.
58. RAMSBOTTOM, J., Work published during 1911 on the cytology of fungus reproduction. Trans. Brit. Mycol. Soc. **3**:354–365. 1911.
59. ———, Recent published results on the cytology of fungus reproduction. Trans. Brit. Mycol. Soc. **4**:127–164. 1912.
60. STOPPEL, R., *Eremascus fertilis*, nov. spec. Flora **97**:333–346. *pls. 11, 12. figs. 6.* 1907.
61. VAN TIEGHEM, P., Sur le développement du fruit des *Ascodesmis*. Bull. Soc. Bot. France **23**:271–279. 1876.
62. ———, Culture et developpement du *Pyronema confluens*. Bull. Soc. Bot. France **31**:355–360. 1884.
63. TUBEUF, KARL VON, Diseases of plants induced by cryptogamic parasites. Eng. edit. by W. G. SMITH. *272–274. figs. 144–147.* 1897 (London, New York, and Bombay).
64. WEIR, J. R., Observations on *Rhizina inflata*. Jour. Agric. Research **4**:93–96. *pl. 8.* 1915.
65. WELSFORD, E. J., Fertilization in *Ascobolus furfuraceus*. New Phytol. **6**:156–161. *pl. 4.* 1907.
66. ———, Conjugate nuclei in the Ascomycetes. Ann. Botany **30**:415–417. 1916.
67. WINGE, O., Encore le *Sphaerotheca Castagnei* Lev. Bull. Soc. Mycol. France **27**:211–219. *pls. 7, 8.* 1911.
68. WOLF, F. A., Spore formation in *Podospora anserina* (Rabh.) Winter. Ann. Mycol. **10**:60–64. *figs. 11.* 1912.
69. WORONIN, M., Zur Entwickelungsgeschichte des *Ascobolus pulcherrimus* Corda und einiger Pezizen. In DEBARY und WORONIN. Beitr. Morph. u. Phys. Pilze. **2**:1–11. *pls. 1–4.* 1866.

EXPLANATION OF PLATES III AND IV

All the figures were drawn with the aid of an Abbé camera lucida, and various combinations of lenses were used. The drawings have been reduced two-sevenths in reproduction. Figs. 1–4 were built up from consecutive sections of a series, two sections each being used for figs. 1 and 2, and three sections each for figs. 3 and 4. This was necessitated by the fact that the archicarp rarely lies for any considerable portion of its length in the plane of one section.

Strictly speaking, however, these drawings are not composite, since the individual cells were outlined as they appear in a single section. In fig. 2 the terminal 6 cells were outlined from one section, and the basal 3 from the adjacent section. All of the central portion of the archicarp shown in fig. 3 was outlined from one section, although portions of these cells appear in the two adjacent sections. This explains the presence in the drawings of the deeply staining pads or open protoplasmic connections at certain septa and their absence at others where they lie outside the plane of the optical section. In those cases in which they are not shown, the examination of other optical sections usually shows either a pad or a pore, but in some cases they are obscured by the dense overlying protoplasm of one or the other of the adjacent cells. In fig. 4, due to the absence of winding in the archicarp, many of the open protoplasmic connections appear in one plane. In drawing the terminal cell of the archicarp shown in fig. 3 an exception has been made to the general method of treatment. This cell on account of its coiled nature cannot be shown satisfactorily in a single plane, but since it lies wholly in one section it has been possible to draw it in perspective. The nuclei shown in figs. 1–4 have not been outlined with the camera lucida, and the writer has attempted to show in the cells of these archicarps merely the relative number and size of the nuclei, not their exact position. The dense nature of the cytoplasm at these stages, the crowding of the nuclei, and the use of several optical sections in the preparation of the drawings renders a faithful portrayal of the nuclei impossible. The remainder of the drawings (figs. 5–27) have been made from a single optical section and the nuclei and other cell contents are accurately reproduced.

PLATE III

FIG. 1.—Terminal portion of young archicarp of *Rhizina undulata* Fries, ×500; note dense protoplasmic contents, numerous nuclei, and deeply staining convex pads on transverse septa of lower and more nearly mature cells; the fact that the terminal cells are long and slender and contain relatively few nuclei indicates the origin of the archicarp from a vegetative hypha.

FIG. 2.—Terminal portion of a somewhat older archicarp, ×500; note attenuated terminal cell, trichogyne; deeply staining pads and open protoplasmic connections cannot be seen on all septa since they lie outside plane of section.

FIG. 3.—An entire archicarp nearing maturity, ×500; 2 ascogonial cells have already begun to put out ascogenous hyphae; deeply staining pads are prominent on several septa; open protoplasmic connections have resulted from their disappearance on others.

FIG. 4.—An entire archicarp contrasted in size with ordinary hyphae of ascocarp, ×500; here open protoplasmic connections are visible at practically every septum.

FIG. 5.—Cells in basal region of archicarp at time of general flow of nuclei and cytoplasm into ascogonial cells, ×500.

FIG. 6.—Cells in apical region of another archicarp when this phenomenon is taking place, ×500.

FIG. 7.—Ascogonial cells of archicarp putting out ascogenous hyphae, ×500; note paired nuclei, and persistence of a single pair of deeply staining pads.

PLATE IV

FIGS. 8, 9.—Transverse sections through budding ascogonial cells at points between places where ascogenous hyphae arise, ×1315; note vacuolated cytoplasm and paired nuclei; no fusion stages have been observed; in those cases in which a solitary nucleus appears, its companion lies either above or below.

FIGS. 10, 11.—Transverse sections through budding ascogonial cells, ×1315; in these cases ascogenous hyphae at their point of origin lie in plane of section; note paired condition of nuclei in ascogenous hyphae.

FIG. 12.—Ascogenous hyphae midway between ascogonial cells and developing hymenium, ×1315.

FIG. 13.—Terminal branches of ascogneous hypha just preceding crozier formation, ×1315.

FIGS. 14–18.—Ascus hooks containing single pair of nuclei preceding conjugate division, ×1315.

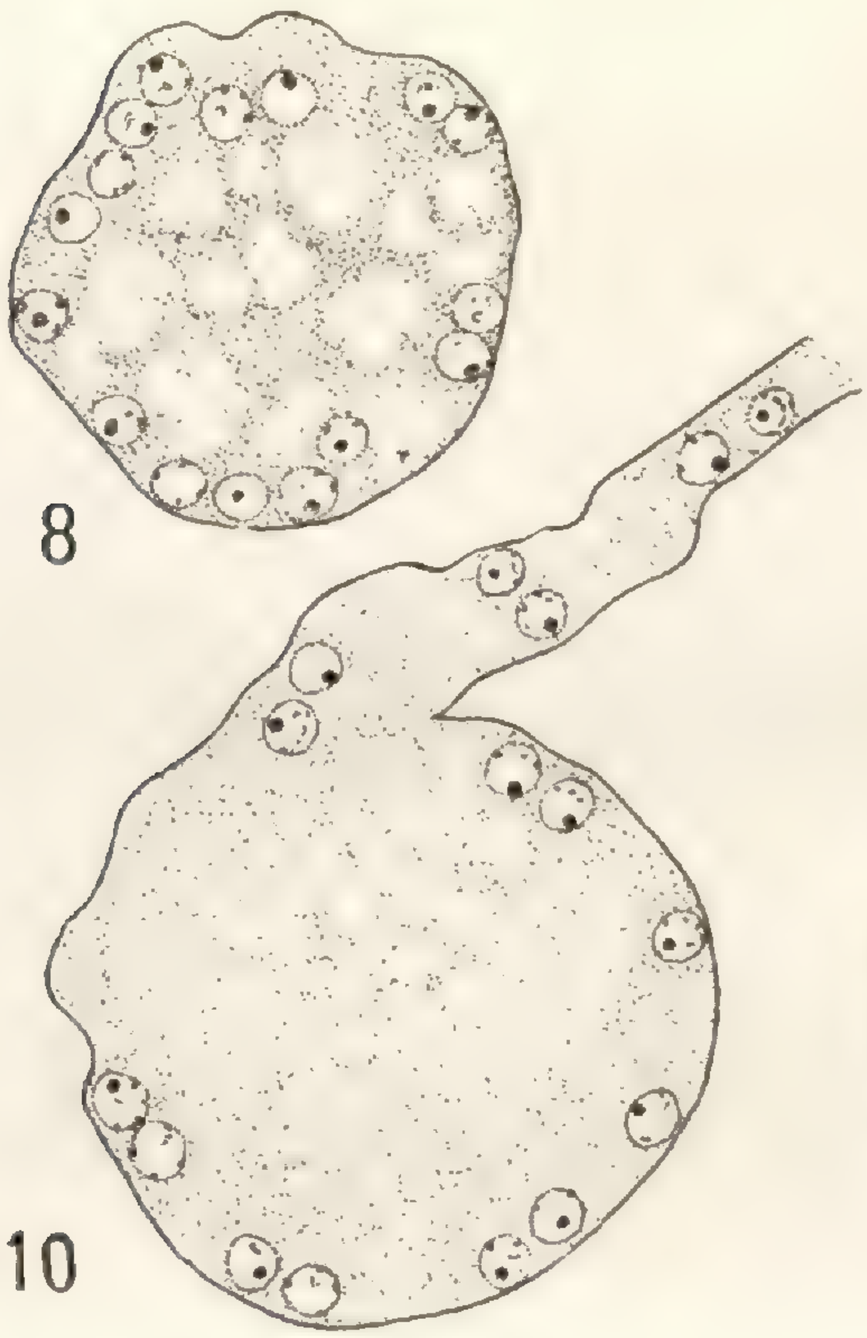
FIGS. 19–21.—Ascus hooks containing 4 nuclei after conjugate division has taken place, ×1315.

FIGS. 22, 23.—Young asci, fusion nucleus in each still showing two nucleoli, ×830.

FIG. 24.—Fusion nucleus containing single fusion nucleolus, ×1315.

FIGS. 25–27.—Young asci showing fusion nucleus with single nucleolus, ×830.

FITZPATRICK on RHIZINA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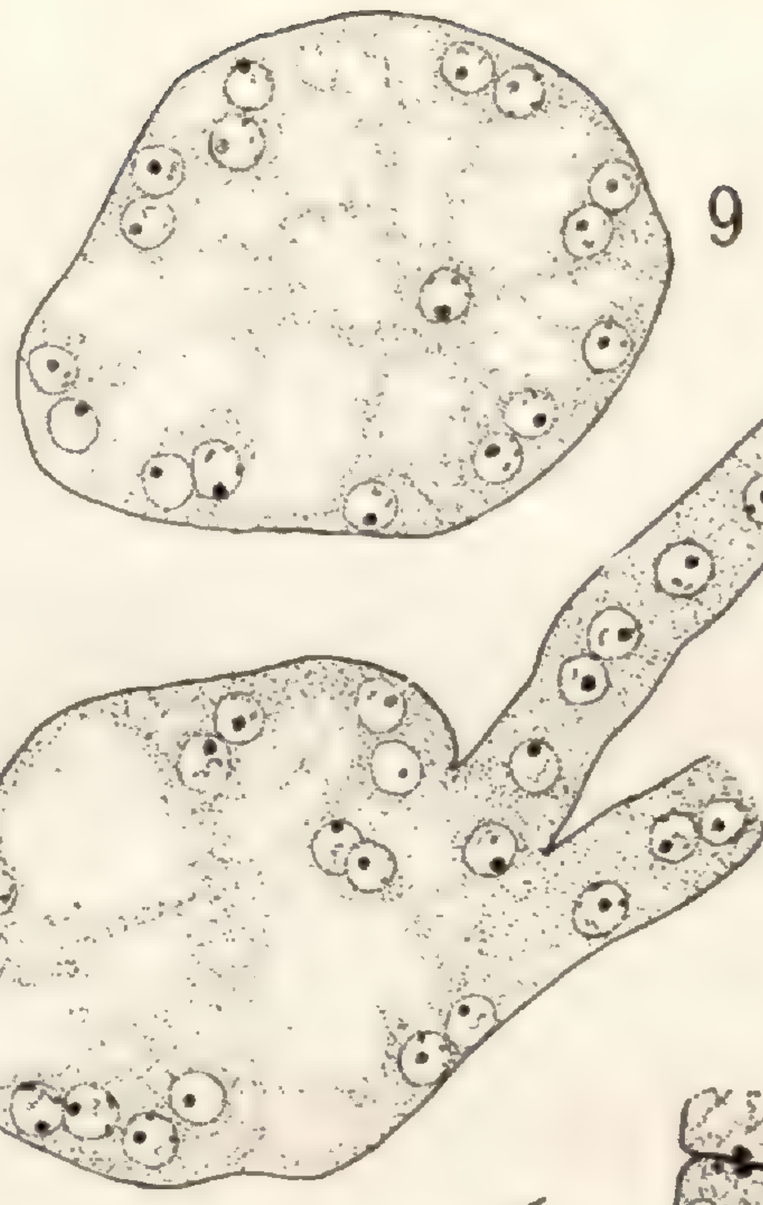
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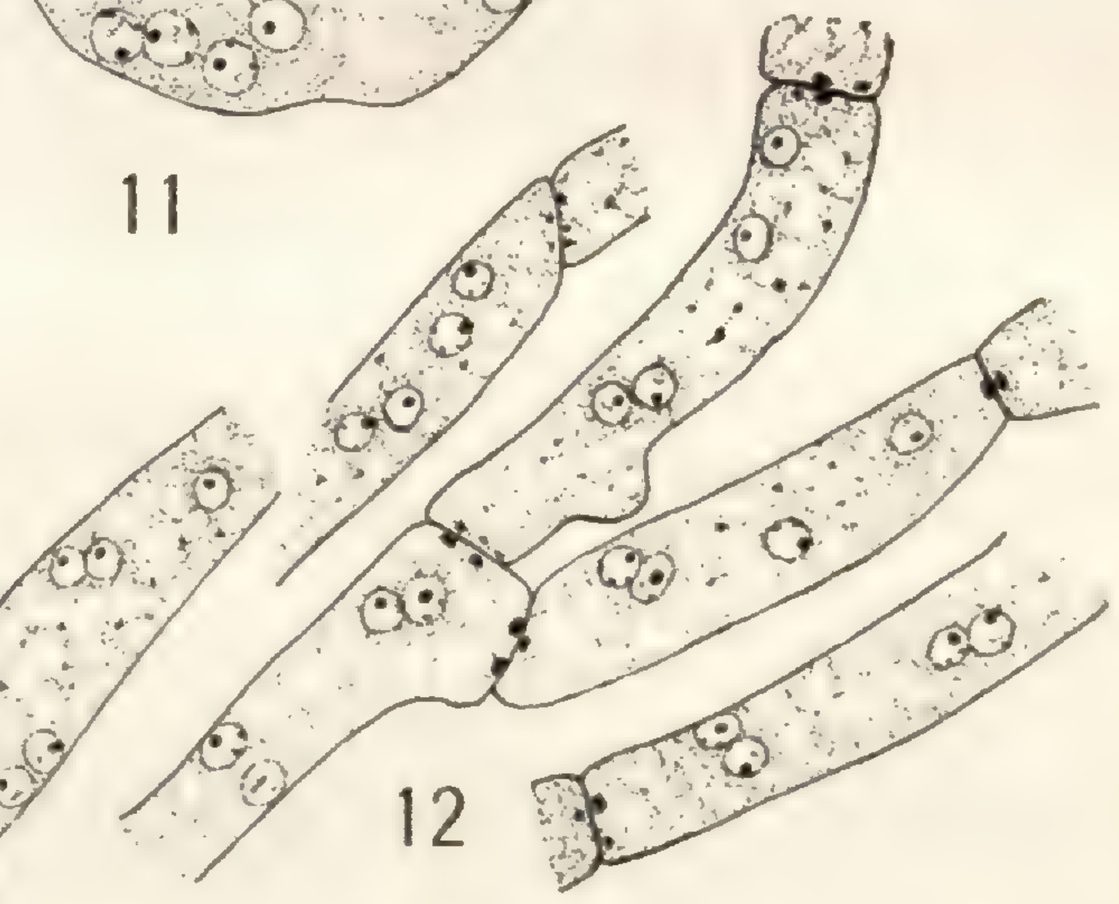
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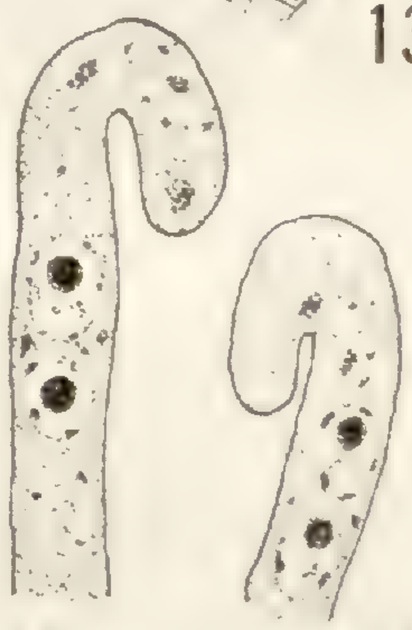
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SOME MELIOLICOLOUS PARASITES AND COMMENSALS FROM PORTO RICO

F. L. Stevens

(WITH PLATES V AND VI AND FIVE FIGURES)

The genus *Meliola* is distinctly tropical and within the tropics is most abundant in humid locations, although there are many species found in arid regions. It is chiefly in the warm humid locations that the species are accompanied and overgrown by other fungi; frequently so heavily overgrown as to entirely obscure the *Meliola* itself, stop spore production, and even the presence of the *Meliola* may be proved only by very careful search. The exact relation which these fungi bear to the *Meliola* is not known. True parasitism, owing to the dark color of the mycelium, is much more difficult to demonstrate than in the case of *Cicinnobolus* on the Erysiphaceae, so familiar in temperate climates. It is extremely probable that all of the forms except the last considered are parasitic. This last is probably merely an accidental associate. Some of the pycnidial forms were formerly regarded as belonging to the *Meliola* cycle, but more recent studies do not support this view. Two of the hyphomycete genera have been regarded by some students of *Meliola* as the conidia of *Meliola*, while others treat them as independent fungi, and still others evade the question.

It is not possible to regard the ascigerous forms of *Microthyrium*, *Dimerium*, *Podosporium*, *Calonectria*, etc., as genetically connected with the *Meliola*, nor is there any more reason for assuming genetic connection in the case of any of the forms mentioned later. They may be merely commensals favored by the environment, but there is very strong circumstantial evidence that they are parasitic, and there is no sufficient reason to regard any of them as belonging to *Meliola*. The special statement in this connection relating to *Arthrobotryum* and *Helminthosporium* is given later. The specimens upon which this article is based are filed under the *Meliola* host, and are deposited as indicated in an article by Miss Young.[1]

[1] Young, E., Mycologia 7:143. 1915.

PEZIZACEAE

BELONIDIUM LEUCORRHODINUM (Mont.) Sacc. on *Meliola chiococcae* Stev. on *Chiococca alba*, 7325, Hormigueros; on *Meliola tortuosa* Wint. on *Piper umbellatum*, 5656, Jajome Alto; on *Meliola rudolphiae* Stev. on *Rudolphia volubilis*, 4835, Maricao, 5439, Luquillo Forest.

This fungus is very inconspicuous and would escape observation except under a good lens. It then appears as numerous small pale disks upon the *Meliola* mycelium. Although the present specimens agree well with the description given in the *Sylloge Fungorum*, there is still some doubt as to its generic position; indeed, the limits of the genera *Calloria* and *Belonidium* are of such nature that this fungus might well be placed in either of them. Although septation of the spores was not definitely proved, there is a segmentation of the protoplasm in the spores which seems to indicate beginning of septation.

PERISPORIACEAE

Perisporium paulliniae, sp. nov. (text fig. 1).—Mycelium inconspicuous. Perithecia few in centers of old *Meliola* colonies. Asci fasciculate from base of perithecium, 100×25 μ, clavate, 8-spored; spores inordinate, clavate to somewhat irregular-cylindrical, 5-septate, 44×10 μ, usually with two cells decidedly thicker than the others; these thickened cells the second and third from one end. Ends obtuse, constriction medium, color dark smoky.

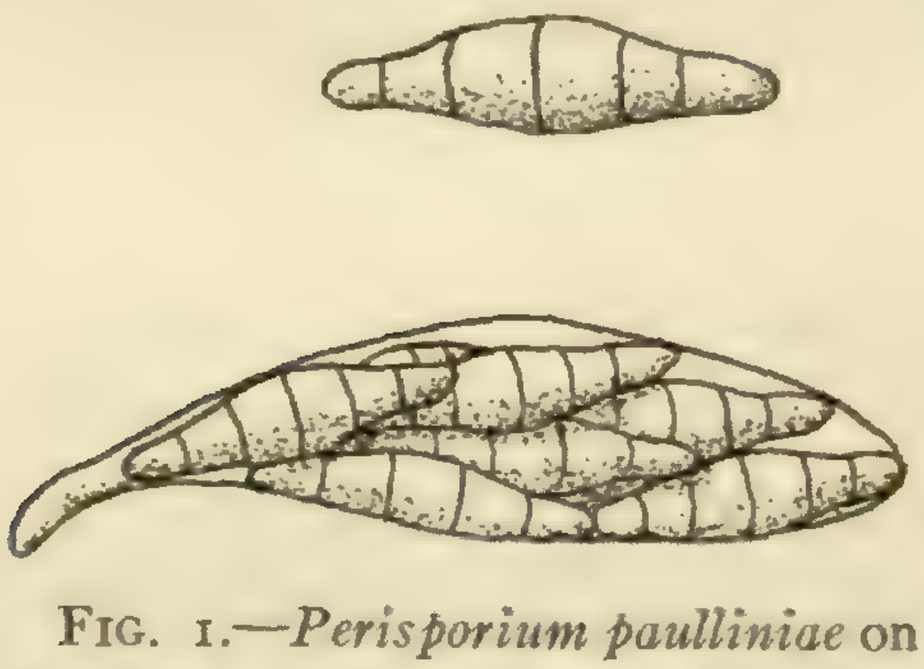

FIG. 1.—*Perisporium paulliniae* on *Meliola hessii*, no. 1207 (type).

On *Meliola hessii* Stev. on *Paullinia pinnata*, 1207 (type), Mayagues.

Perisporium meliolae, sp. nov. (text fig. 2).—Mycelium scant, inconspicuous, growing upon *Meliola* mycelium. Perithecia clustered in the central regions of old *Meliola* colonies, lenticular, slightly taller than broad, 230–280 μ thick, 312 μ high, surface closely covered with short tubercles. Asci numerous, fascicled, 8-spored, cylindrical. Paraphyses absent. Spores 7–14×31–44 μ,

brown, usually 3-septate (sometimes less), often tapering toward one end, that is, ends not equally thick. Ends obtuse, median constriction greater than the others, wall thick, 2–3 μ, surrounded by a distinct, thin, gelatinous coat.

On *Meliola compositarum* var. *portoricensis* Stev.; on *Eupatorium portoricense*, 6032 (type), 6557, 6056, 6003, 6861, 6031, 6866, Dos Bocas near Utuado, 5192, San Sebastian.

The presence of the 8-spored, fascicled, long, narrow asci and the absence of the typical *Meliola* mycelium distinguish this *Perisporium* from *Meliola*. The peculiar lenticular perithecia, which stand on edge, are also characteristic. Associated with this species are conidiophores and conidia, and it is entirely probable that it may be the ascigerous stage of one of the Meliolicolous species of *Helminthosporium*.

FIG. 2.—*Perisporium meliolae* on *Meliola compositarum* var. *portoricensis*. no. 6032 (type); flattened perithecium; views from side, edge, and from above; an ascus and single spore.

These two species of *Perisporium* are especially interesting, since, growing on *Meliola*, their perithecia are likely to be taken for the *Meliola* perithecia, which they closely resemble in character of spores. They are readily separable, however, from *Meliola* by the absence of the characteristic *Meliola* hyphopodia and by the presence of the fascicled, 8-spored asci which perhaps do not really occur in true *Meliola*.

DIMERIUM PICEUM (B. and C.) Thiessen Bot. Centralbl. Beih. **29**:66. 1912.—*Asterina picea* B. and C.; *Dimerium microsporium* Speg.; *D. meliolicolum* Speg.; *D. guineri* R. Marie; *Dimerosporium tropicale* Speg.; *D. clidemniae* P. Henn.; *D. hyptidicola* P. Henn.; *D. dendriticum* A. and S.

On *Meliola glabra* var. *psychotriae* Stev. on *Psychotria* sp., 5032, Quebradillas; on *Palicourea* (?) 1070, Mayaguez. On *Meliola bicornis* Wint. on *Meibomia supina*, 4532, Cataño. On *Meliola glabroides* Stev. on *Piper aduncum*, 4802, Maricao. On *Meliola tortuosa* Wint. on *Piper umbellatum*, 3379, Maricao. On *Meliola ipomoeae* E. Heller's coll. no. 6285 appears to be the same, but the available material is scarce. On *Meliola compositarum* E. var.

portoricenis Stev. on *Eupatorium portoricense*, 6031, Utuado. On *Meliola pteridicola* Stev. on *Aneimia adiantifolia*, 7269, Quebradillas, 8015, Utuado, 7814, Rio Tanamá. On *Meliola panici* E. on *Panicum glutinosum*, 4801, Maricao; on Gramineae indet., 6796, Arecibo; on *Lasiacis divaricata*, 4298, Manati. On *Meliola paulliniae* Stev. on *Casearia ramiflora*, 6683, St. Ana, 5844, San German.

While slight variations occur, it seems best to do as THIESSEN has done and regard the variants as of one species, and to unite the several species which were originally described as distinct.

MICROTHYRIACEAE

Members of this family abound on *Meliola*. The manner in which the mycelium of the parasite clothes the mycelium of the *Meliola* in a sheath is particularly striking. In some instances only single *Meliola* branches, portions of a colony, are so coated; in other cases the whole *Meliola* colony is covered. Sometimes the sheathing is limited to the host mycelium, but in older specimens the sheath expands into a continuous sheet or crust. The perithecia are very numerous, on young colonies as very small developing structures, on old ones as dense clusters of mature perithecia. Several species of *Meliola* have been described as having this crustose structure, and it is very probable that all such cases represent merely parasitized colonies. Generic and specific determination of the specimens is deferred for consideration in a separate paper dealing with the family.

HYPOCHREALES

Pseudonectria pipericola, sp. nov.—Mycelium closely appressed on the *Meliola* mycelium. Perithecia numerous, minute, 100–125 μ in diameter, pink, with a few setae around the ostiole. Setae short, 20–30 μ, obtuse, continuous; asci cylindrical, 50×5–7 μ, 8-spored, 1-seriate, sometimes oblique; paraphyses none; spores elliptical or oblong, obtuse, continuous, hyaline, 9–10×3–4 μ.

On *Meliola tortuosa* Wint. on *Piper umbellatum*, 5656 (type), Jajome Alto, 3578, 3508, 3507, Añasco, 7916, 7848, Rio Tanamá; on *Piper marginatum*, 7777, 7842, Rio Tanamá.

This is closely related to *Nectria mycelophila* Pk. described on decaying fungi, but differs in having smaller spores, different shape of asci, and in the presence of setae around the ostiole.

Nectria meliolicola, sp. nov.—Amphigenous, spot none, mycelium white, closely appressed to the *Meliola* mycelium and to the leaf, usually coextensive with the *Meliola* or slightly exceeding it. Perithecia very minute, 50–60 μ at center or near edge of colony, hyaline, hairy at apex, hairs 15 μ long. Asci ovate to elliptical, obtuse, stipitate, 40–45×11–14 μ; spores 1-seriate, oblique, 1-septate, hyaline, linear, 24–28×3–4 μ, acute.

Associated with an undetermined *Fusarium* on *Meliola paulliniae* Stev. on *Casearia sylvestris,* 1051, Mayaguez (type).

It is impossible to distinguish the mycelium of this fungus from that of the *Fusarium*, and it is probable that the two are one. The spot caused on the leaf is not due to these fungi but to the *Meliola.*

Nectria portoricensis, sp. nov.—Colonies approximately circular on *Meliola*, 3–7 mm. in diameter, white, central portion bearing perithecia, outer part sterile. White mycelium covering each *Meliola* strand with a shaggy coat. Perithecia red, small, 160 μ, smooth; asci 25–36×8 μ, obovate, obtuse; spores 1-seriate, oblique, oblong, hyaline, pale to green, 1-septate, 12×3 μ, obtuse.

Distinguished from *N. pipericola* P. Henn. by absence of perithecial setae, shape and size of spores, and by habit of the sterile mycelium; from *N. bakeri* Rehm. by spore characters. On *Meliola rectangularis* Stev. on *Banisteria laurifolia*, 1001, Jayuya (type).

This fungus differs strikingly from all other Porto Rican Nectriaceous fungi in the beautifully arranged, dense, shaggy, white mycelial coating which drapes with geometrical accuracy every affected strand of the *Meliola* mycelium. A white mycelium of appearance similar to this was abundant, overgrowing colonies of *Meliola melastromacearum* Speg. no. 7037, but no perithecia were seen.

CALONECTRIA MELIOLOIDES Speg.

On *Meliola compositarum* var. *portoricensis* Stev. on *Eupatorium portoricense*, 6003, 6032, 6557, 6830, 6031, 6861, 6866, 7953, 8102, Dos Bocas below Utuado, 5192, San Sebastian; on *Eupatorium odoratum*, 6001, 6056, 6574, Utuado. On *Meliola paulliniae* Stev. on *Casearia sylvestris*, 3920, 1200, Mayaguez. On *Meliola hessii* Stev. on *Paullinia pinnata*, 1207, Mayaguez.

Spores on this host showed a pale olivaceous tint. The form on *Eupatorium portoricense* usually forms a mat of densely felted mycelium and may be a distinct species. On *Meliola monensis* Stev. on *Amyris elemifera*, 6158, Mona Island.

CALONECTRIA ERUBESCENS (Rob.) Sacc.

On *Meliola bicornis* Wint. on *Meibomia supina*, 5820, Adjuntas. On *Meliola tortuosa* Wint. on *Piper umbellatum*, 5692, Jajome Alto. On *Meliola cupaniae* Stev. on *Cupania americana*, 9318, Mayaguez.

Calonectria graminicola, sp. nov.—Mycelium growing over the *Meliola* and covering it with a white coat, usually coextensive with the *Meliola*. Perithecia few to numerous, reddish, pale when dry, globose, 200–225 μ, cells irregular, 10–18 μ in diameter. Perithecial setae rather numerous, tapering regularly to an obtuse apex, not septate, base not bulbous although swollen slightly just above attachment, 75 μ long, 15 μ wide at base. Asci numerous, 8-spored; 75×7–8 μ, cylindrical; paraphyses threadlike, abundant. Spores 3-septate when mature, hyaline to pale straw colored, straight, curved or sigmoid, acute at each end, 30–36×5 μ.

On *Meliola panici* Earle on *Lasiacis compacta*, 4663 (type), Utuado; on *Lasiasis divaricata*, 4298, Manati, 6796, Arecibo. On *Meliola andirae* E. on *Andira jamaicensis*, 5269, Manati.

This fungus resembles *C. melioloides* Speg., but may readily be distinguished by its non-septate setae and the shape of the spores.

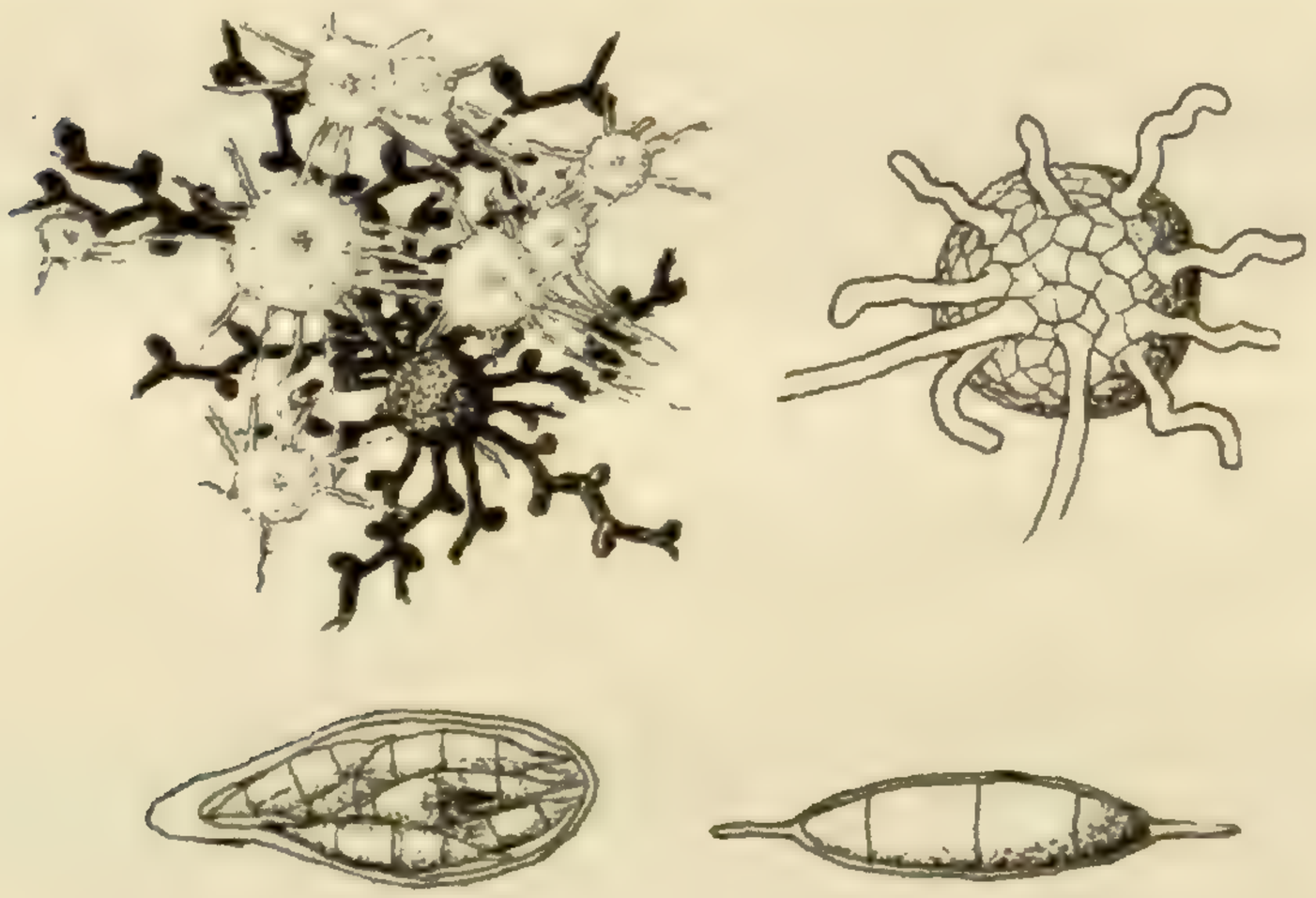

FIG. 3.—*Paranectria meliolicola*, sp. nov.: *a*, ascus, *b*, single spore.

One of the Hypocreales, probably a *Calonectria* but immature and therefore not determinable, was profuse on *Meliola toruloidea* Stev. on *Cassia quinquadrangulata*, 8394, Jajome Alto.

Paranectria meliolicola, sp. nov. (text fig. 3).—Mycelium hyaline, of threads 5 μ thick, which closely surrounded the *Meliola* mycelium. Perithecia produced in abundance, 75–120 μ in diameter, red to pale, with few setae, 15–30–50 μ long. Asci clavate to ovate, obtuse, 8-spored,

thin-walled, 45–55×25–40 μ. Spores hyaline, oblong to oblong-elliptical or with one side nearly straight and the other arched; ends obtuse, a rigid, obtuse, straight, sometimes slightly curved awn at each end. Spores 3-septate, 2 outermost septa arched strongly outward, spore body 7–10×22–30 μ; awn 2×8 μ.

On *Meliola tortuosa* Wint. on *Piper umbellatum*, 3634, Maricao (type). On *Meliola glabroides* Stev. on *Piper aduncum*, 4930, Lares.

This interesting genus differs from *Calonectria* only in the possession of appendaged spores. There are less than 10 species, none of which agrees at all closely with ours. *P. albo-lanata* Speg. described on bamboo does agree closely in spore character but not otherwise. The fungus without the use of a lens is barely visible.

Paranectria miconiae, sp. nov. (text fig. 4).—Perithecia globular, gray to white, 100–150 μ in diameter, with a whorl of basal hairs which are non-septate, thick-walled, obtuse; in length equal to

FIG. 4.—*Paranectria miconiae*, sp. nov.: *a*, habit sketch showing *Paranectria* overgrowing *Meliola; b*, perithecium seen from below, showing basal hairs; *c*, spores on microthyriaceous fungus on *Miconia;* no. 6705.

half the diameter of the perithecium. Asci numerous, clavate to ovate, obtuse, thin-walled, 60×12–15 μ. Spores fusiform, strongly thickened in middle and tapering equally to each end. Almost long diamond-shaped in outline, with a straight, cylindrical awn at each end, 32×7–8 μ including awns, 3-septate. Spores in mass, or in ascus, slightly greenish. Paraphyses threadlike, short.

On *Miconia* on Microthyriaceous fungus, 6705, Yabucoa (type).

SPHAEROPSIDALES

Naemosphaera hyptidicola, sp. nov.—Pycnidia spherical, about 60 μ in diameter, black, mycelium inconspicuous. Rostrum long, often 500 μ, 17 μ thick, dark, tip pale, composed of parallel hyphae. Spores straw colored, oblong, obtuse, 5–6×2.5–3 μ.

On *Meliola hyptidicola* Stev. on *Hyptis*, 5760, Monte de Oro (type).

This does not agree with any pycnidial forms given by GAILLARD as occurring on *Meliola;* 3 only of his are yellow spored, namely, those on *M. ganglifera*, *M. cladotricha*, and *M. furcata*. The first two have large spores, and the length of neck of the pycnidium on my species does not agree at all with any of the three. *N. hyptidicola* is also distinct from the rather closely allied genus *Cicinobella* recorded as parasitic on *Parodiella*.

Coniothyrium glabroides, sp. nov.—Pycnidia small, 50–90 μ, brown, ostiole distinct, no beak; mycelium inconspicuous; spores brown, 4–5×3.5 μ, obtuse, oblong.

On *Meliola glabroides* Stev. on *Piper aduncum*, 4802 (type). On *Meliola tortuosa* Wint. on *Piper umbellatum*, 3379, Maricao; also on no. 6258 of the Heller collection and on *Meliola compositarum* E. and no. 6185 of the Heller collection. On *Meliola guareicola* Stev. on *Guarea trichilioides*, 8166, Las Marias. On *Meliola arecibensis* Stev. on *Acalypha bisetosa*, 6547, near Utuado. On *Meliola compositarum* var. *portoricensis* Stev., 6032, on *Eupatorium portoricense*.

This fungus bears resemblance to *Cicinobella*, but the ostiole does not protrude. The spores too are different in size from the only species of that genus described. Specimens on *Meliola panici* E. on *Lasiacis divaricata*, no. 4298, Manati, agree closely with the preceding except that the spores are hyaline. I take them to be immature and place the specimens under this name. The same is true of specimen 7269, Quebradillas, on *Meliola pteridicola* Stev. on *Aneimia adiantifolia*.

In the closely allied genus *Chaetophoma* the following species have been described on *Meliola* and related genera.

C. foeda Sacc. on *Capnodium*, *C. penzigi* Sacc. on *M. penzigi*, *C. citri* Sacc. on *M. citri*, *C.*(?) *ampullula* Speg. on *M. dubia*, *C.*(?) *asterinum* Speg. on *Asterina* sp., *C. perpusilla* Speg. on *Asterina pseudopelliculosa*, *C. meliolicola* Speg. on *Dimerosporium*.

GAILLARD mentions pycnidial fungi on the following species of *Meliola: M. ganglifera, M. cladotricha, M. penicilliformis, M. ambigua, M. desmodii, M. furcata, M. dichotoma.*

MONILIALES

Acremonium meliola, sp. nov.—Mycelium copious, white to salmon colored, forming cottony blotches on leaves where it overgrows *Meliola*, fine, 3 μ, septate, hyaline. Conidiophores smiliar to the mycelium, erect or ascending, often simple or with dichoto-

mous or verticillate branching. Conidia terminal and solitary or more rarely in clusters, pear-shaped, rounded or obtuse at base, acute at apex, 15–20×5–7 μ. Spores, mycelium, and conidiophores encrusted with minute granules.

On *Meliola paulliniae* Stev. on *Paullinia pinnata*, 376, Vega Baja.

This is clearly differentiated from the other species by the shape of the spores.

Arthrobotryum Ces.

The forms here under discussion are characterized by fuscous to dark mycelium, conidiophores, and spores; conidiophores long, straight, and fascicled in typical coremia. The coremia are in the main straight and rigid, the component fibers running approximately parallel and are firmly agglutinated. They are not sporiferous upon the lower parts, but possess a well marked, long, nonsporing stipe. The extreme distal parts of the coremia are usually swollen to more or less cylindrical or conical heads, although in some species the head is but poorly developed. The spores are elliptical or falcate, 2 or 3-septate, fuscous. Such structure clearly places these forms in the Stilbaceae-Phaeostilbeae-Phragmosporae. They are usually regarded as belonging to the genus *Podosporium*, and 3 species growing on *Meliola* have been described: *P. penicillium* Speg. (Fung. Arg. Pug. IV. n. 117), *P. penicillioides* Karsten and Roum. (Rev. Myc. **12**:77. 1890), *P. densum* Pat. (Jour. de Botanique **11**:373. 1897). Examinations of original figures of the type species of this genus (*P. rigidum* Schw. Syn. Amer. Bor, n. 2608, Trans. Am. Phil. Soc. n.s. 4) and of a specimen of Ellis (N.A.F. no. 416), which agrees with description and type figure fully, shows the *Podosporium* coremium to be pleurogenous and without heads, and therefore to be clearly distinct generically from the forms under discussion.

Comparison with figures of the type species of *Arthrobotryum* Ces., *A. stilboideum* (Engler and Prantl, Die Nat. Pflanzenfam. **1**: pt. 1. *fig. 257D*), and with figures of later species placed in this genus (Jour. Linn. Soc. **35**:13. *pl. 1. figs. 13–15*. 1901) show complete generic agreement.

While these structures have been regarded by some as independent species of fungi growing as parasites upon *Meliola*, Gaillard

and others who have followed him regarded them as belonging to *Meliola* and constituting one of its conidial forms. The question is very complex and difficult and reminds one of the old lichen arguments.

The undisputed facts are as follows: *Meliola* possesses a relatively coarse mycelium characterized by capitate and mucronate hyphopodia. This mycelium bears perithecia, sometimes setae. Occasional species sometimes have this coarse mycelium densely entwined with a very fine mycelium entirely without hyphopodia, more pale in color, and different in every way from the first. This fine mycelium gives rise to conidiophores, simple or coremioid. To all appearances two distinct fungi are present, as was assumed by the earlier authors. The ascospores on germination nearly always immediately give rise to the typical coarse mycelium. The conidia always give rise to the fine mycelium. GAILLARD (Le Genre *Meliola*, 1892, *pl. 3. fig. 2*), however, figures, and I have several times seen, ascospores which have germinated by a somewhat finer mycelium than usual, one devoid, so far as observed, of hyphopodia. He reasons from this that the two types of mycelium are from the same parentage, the ascospore, and that therefore the conidia belong to *Meliola*. This variation from the normal mode of germination is really all the evidence that he had for this conclusion.

I believe that this evidence fails completely for two reasons. First, the fine mycelium which GAILLARD figures originating from the ascospores and which I have studied closely is not at all like the conidiiferous mycelium; it is distinctly coarser, darker (facts which come out clearly in GAILLARD'S own pictures; compare his *pl. 3, figs. 3a* and *2a* with *pl. 4, figs. 3* and *1d*), and moreover there is no evidence whatever that it does produce conidia. I regard it merely as a weak *Meliola* mycelium. Second, I find this abnormal, unusual type of germination on species of *Meliola* which show no conidia; notably on *M. andirae* (cotype slide) and *M. rudolphiae* (specimen no. 8698). These facts, together with a study of more than 700 collections, and extensive field and laboratory observations of *Meliola* embracing many of these conidial stages, convince me that the fine and the coarse mycelia are from distinct and independent fungi; that the conidia do not belong to *Meliola* but to a

fungus parasitic upon it; and, as just stated, that the stilboid conidial forms belong to the genus *Arthrobotryum*. That this conclusion has also been reached by SYDOW[2] is indicated by his description of *A. caudatum* on *Meliola* in 1909. The type specimen of *A. caudatum*, loaned to me by SYDOW, clearly is cogeneric with the various forms on *Meliola* which have heretofore been called *Podosporium*. I present the following synopsis of the Porto Rican forms of this genus:

KEY TO PORTO RICAN SPECIES OF *Arthrobotryum*

Coremia incasing the *Meliola* setae.....*A. dieffenbachiae*
Coremia not incasing the *Meliola* setae
  Vegetative mycelium closely sheathing the *Meliola* mycelium..*A. glabroides*
  Vegetative mycelium not closely sheathing the *Meliola* mycelium
    Conidia long, elliptical, with no distinct beak cell.....*A. penicillium*
    Conidia with distinct beak cell, basal cell, and two central cells
A. caudatum

Arthrobotryum dieffenbachiae, sp. nov. (fig. 4).—Mycelium inconspicuous, scant, fine, pale, tufted around the bases of the coremia. Coremia often growing incasing the setae of the host, yellow, stalks 17–31 μ thick; total length 470–630 μ; apical portion either broadened into a fan-shaped brush or very narrow with lateral conidia; sporiferous part about 150 μ long. Conidia 3-septate, pale straw colored, pointed at each end, apical cell longer than basal cell, 35–38×3–4 μ.

On *Meliola dieffenbachiae* Stev. on *Dieffenbachia sequina*, no. 8077 (type), Dos Bocas below Utuado.

This species is the only one recorded which utilizes the setae of its host as supports for the coremia. The young coremia are somewhat transparent, and in them the supporting setae with their characteristically branched apices may be seen incased.

Arthrobotryum glabroides, sp. nov. (figs. 1–3).—Mycelium forming a loose network on the leaf surface but a close sheath over the *Meliola* mycelium. so dense as to partially obscure the hyphopodia, very fine, about 1 to 1.5 μ. Coremia straight, rigid, black, stalk about 24 μ thick, head 85 μ wide and 85 μ long, top-shaped. Total length of coremia 550 μ. Conidia narrowly elliptical, acute

[2] SYDOW in DE WIDEMAN'S, EMILE DE, Fl. Bas et Moy., Congo pl. III, fasc. 1, 1909.

at each end, dark brown when mature, 17–21×3.5 μ, typically 3-septate with the two terminal cells much smaller than the other cells.

On *Meliola glabroides* Stev. on *Nectandra patens*, no. 7595 (type), Mayaguez, 8867, Maricao.

This species is quite distinct from all others seen in the characteristic manner of sheathing its host, also in the shape of the conidia.

Arthrobotryum penicillium (Speg.), comb. nov.—*Podosporium penicillium* Speg. Fung. Puigg., n. 471.

On *Meliola panici* E. on *Panicum glutinosum*, 5672, 5746, 5560, Monte de Oro, 4375, Ponce, 5947, El Gigante, 4801, 8934, Maricao, 4368, El Alto de la Bandera, 4389, Utuado; on *Lasiacis divaricata*, 4298, Manati, 6810, Arecibo; on *Ichnanthus pallens*, 7441, Mayaguez, 5755, Monte de Oro; on Gramineae indet., 6796 Arecibo.

This form was originally described by SPEGAZZINI as the conidial stage of *Meliola penicillata*, and was later regarded by GAILLARD as the conidial stage of *M. calva*.

ARTHROBOTRYUM CAUDATUM Syd. (figs. 5–7).—A portion of the type specimen was sent to me by SYDOW, and its agreement with the specimens mentioned below is obvious.

On *Meliola pteridicola* Stev. on *Aneimia adiantifolia*, 8015, near Utuado. On *Meliola paulliniae* Stev. on *Casearia ramiflora*, 512, 7745, Vega Baja, 9306, Barcelonata. On *Meliola didymopanicis* P. Henn. on *Dendropanax laurifolium*, 8265, El Alto de la Bandera. On *Meliola glabra* B. and C. var. *psychotriae* Stev. on *Palicourea*, 6650, near Utuado, 468, Vega Baja; on *Psychotria pubescens*, 8032, near Utuado, 7741, 7732, Vega Baja; on *Psychotria bertiana*, 8646, 8566, 8528, El Gigante, 8278, 8673, El Alto de la Bandera; on *Palicourea*, 1070b, 316, Mayaguez; on *Psychotria* sp., 5032, Vega Baja, 5944.

What appears to be the same fungus was described as the conidial stage of *M. penicilliformis* by GAILLARD (Le Genre *Meliola*, 57, 1892). The species of *Meliola* itself being largely determined by its "conidial stage," its validity may well be doubted.

The specimens following seem to agree with the preceding in all respects except that the coremia are usually pale at tip, apparently soft, with the base tan or darker, the head merely a somewhat thickened apical region and the conidia very pale. It seems that the fungus on *Palicourea* shows transition forms which connect the two types.

On *Meliola hyptidicola* Stev. on *Hyptis lantanifolia*, 8130, Las Marias; on *Hyptis* sp., 5760, Monte de Oro. On *Meliola longipoda* Gaill. on *Anona montana*, 7561, Mayaguez. On *Meliola glabroides* Stev. on *Piper aduncum*,

9334, Martin Peña. On *Meliola ambigua* Pat. and Gaill. on *Lantana*, 6870, near Utuado.

The species on *M. glabroides* shows some variation in that the coremia usually taper gradually from the base to tip and are mounted upon a small tuft of radiating, fine, mycelial threads.

What appears to be the same species, although sterile, is on *Meliola psychotriae* E. on *Gonzalugunia spicata*, 9134, Miradero, 7592, Mayaguez, and on *Meliola melastomacearum* Speg. on *Miconia leavigata*, 8085, near Utuado, and on *Miconia racemosa*, 7636, 7414, Mayaguez. On *Meliola bicornis* Wint. on *Meibomia supina*, 8975, 8793, Maricao.

In addition to these the genus *Arthrobotryum*, under the name of *Podosporium*, has been noted as *P. densum* on *Meliola* sp. indet., as *P. penicillioides* on *Meliola tonkinensis;* while upon the following species of *Meliola* it has been described as a conidial stage: *M. echinata*, *M. insignis*, *M. glabra*, *M. quercina*.

Helminthosporium Link

Closely allied to *Arthrobotryum* is the genus *Helminthosporium*, which indeed, so far as it is parasitic upon *Meliola*, may be regarded as a simple form of *Arthrobotryum;* that is, in *Arthrobotryum* the conidiophores are fascicled in coremia, while in *Helminthosporium* the conidiophores are not so fascicled. In spore forms, in mycelial characters, and in all respects except the fasciculation of the conidiophores, the two genera as they occur on *Meliola* are identical. They bear the same relation to each other as do the form genera *Coremium* and *Penicillium*, a relation which emphasizes strongly the artificiality of a taxonomic system which separates widely forms which are in reality very closely related. The assumed genetic connection of *Helminthosporium* with *Meliola* has been sufficiently discussed under *Arthrobotryum*. The facts stated in that connection may be considered as applying equally to the forms now under discussion.

The Meliolicolous species of *Helminthosporium* are typical representatives of the genus. The mycelium is very fine, sometimes scant and diffuse, more often dense and matted. The conidiophores are commonly solitary, usually although not always much darker than the mycelium, and always considerably thicker than the mycelium. Their origin from the mycelium is well shown in

pl. 7, fig. 1 of GAILLARD'S *Le Genre Meliola*. They are in a few forms somewhat tufted, and what are apparently transition forms to *Arthrobotryum* occur. The conidia are in most species truncate at one end, beaked at the other. The beaked end is apical and the truncated end is basal, although the reverse condition might be assumed were the spores not studied *in situ* (see fig. 10); in the 3-septate forms the terminal cells are usually more pale than the central cells. The following key will serve to separate the Porto Rican species:

Conidia often more than 3-septate
  Conidiophores not very toruloid at tip.....*H. glabroides*
  Conidiophores very toruloid at tip.....*H. guareicolum*
Conidia not often more than 3-septate
  Conidiophores pale, translucent.....*H. ocoteae*
  Conidiophores not pale and translucent
    Conidia usually not strongly differentiated at two ends
      Conidiophores 280 μ.....*H. melastomacearum*
      Conidiophores 170 μ.....*H. panici*
    Conidia differentiated strongly at two ends
      Beak short, usually 7 μ.....*H. parathesicolum*
      Beak longer, usually 7 μ or more
        Conidiophores thick, 7 μ.....*H. helleri*
        Conidiophores thin, 4 μ.....*H. philodendri*

Helminthosporium glabroides, sp. nov. (figs. 8–10).—Mycelium very fine, pale, almost hyaline, conidiophores solitary, but often close together, about 100–140×7 μ, dark, sometimes pale at apex, often bent but not toruloid. Conidia 3–6-septate, 40–81×6–7 μ, truncate at base, tapering at apex.

On *Meliola glabroides* Stev. on *Piper aduncum*, 9039, El Alto de la Bandera (type), 4390, Lares, 3582, Añasco, 3647, Maricao, 4802, 3371, 7297, Arecibo, 8471, Aibonito, 9603, Las Marias. The long conidia on this host are quite typical, with a truncate base and gradually tapering toward the apical end. Occasionally smaller, 3-septate spores are seen. These are shorter, proportionately thicker, and have a long apical cell. The variation from the long, many-celled spore to the shorter 3-celled one is sometimes striking. In one part of the microscope field one form may predominate, while in another part of this field the other spore form is dominant.

On *Meliola comocladiae* Stev. on *Comocladia glabra*, 7484, 7056, Mayaguez, 760, Maricao. The conidiophores are darker than in the type and are sometimes slightly toruloid. Occasionally there is a strong tendency for them to be in groups.

On *Meliola hessii* Stev. on *Paullinia pinnata*, 1207b, Mayaguez. On *Meliola didymopanicis* P. Henn. on *Dendropanax arboreum*, 7440. On *Meliola polytricha* K. and C. no. 1256 (type specimen loaned from the Kew collection). No "conidial stage" was described for this by GAILLARD, although the type specimen contains abundant conidia, and these are mentioned by the authors of the species.

On *Meliola laguncullariae* E. on *Conocarpus erecta* L., 9201, Guanajibo. On *Meliola longipoda* Gaill. on *Tournefortia hirsutissima*, 7965, near Utuado. On *Meliola gesneriae* Stev. on *Cestrum laurifolium*, 824, Maricao. On *Meliola maricaensis* Stev. on *Ilex nitida*, 3679, 3607, Maricao. On *Meliola compositarum* var. *portoricensis*. Stev. on *Eupatorium portoricense*, 7320, Arecibo-Lares Road, 7723, Vega Baja, 6031, 6032, near Utuado; on *Eupatorium odoratum*, 6056, near Utuado. On *Meliola psychotriae* E. on *Chiococca alba*, 9299, Martin Peña, 7859, Rio Tanamá, 7467, Mayaguez. Conidia on this host are somewhat shorter than in the type. The conidiophores on no. 9299, and other specimens are sometimes quite strongly tufted, but they often grow singly as well.

On *Meliola puiggiarii* Speg. on Rubus, 8650, El Alto de la Bandera. On *Meliola gaillardiana* Stev. on *Piper aduncum*, 8225, Las Marias, 7796, Rio Arecibo. On *Meliola pteridicola* Stev. on *Aneimia adiantifolia*, 7814, Rio Tanamà, 7269, Quebradillas; on *Adiantum latifolium*, 8182, Las Marias, 7418, Mayaguez. On *Meliola toruloidea* Stev. on *Cassia quinquadrangulata*, 8394, Jajome Alto. On *Meliola monensis* Stev. on *Amyris elemifera*, 6150, Mona Island. On *Meliola nigra* Stev. on *Laguncularia racemosa*, 7197, Guanajibo.

This species is clearly differentiated from all other Porto Rican forms, and from all forms previously described associated with *Meliola*, by the long, narrow, many-septate conidia.

Helminthosporium guareicolum, sp. nov. (fig. 16).—Mycelium abundant, fine, pale. Conidiophores many, dark, basal part rigid, straight, upper part very torulose often for considerable distance (70 μ or more). Conidia truncate at base, beaked at apex, 3 or more septate.

On *M. guareicola* Stev. on *Guarea trichilioides*, 8166, Las Marias (type) 8096, Utuado.

Helminthosporium ocoteae, sp. nov.—Mycelium fine, pale straw color, diffuse. Conidiophores pale straw color, translucent, septate, tips crooked, 135–200×4 μ. Conidia 3-septate, 20–28× 4–6 μ.

On *Meliola ocoteae* Stev. on *Ocotea leucoxylon*, 8428, Jajome Alto (type).

The distinguishing character of this species is in the pale, translucent conidiophores.

Helminthosporium melastomacearum, sp. nov. (fig. 11).—Mycelium very fine, 1–1.5 μ, reticulated. Conidiophores abundant, black, lax, long, thin, 280×3 μ. Conidia narrowly elliptical, 3-septate, acute at each end, 14–21×3.5–6 μ.

On *Meliola melastomacearum* Speg. on *Miconia racemosa*, 7389, Mayaguez (type). On *Meliola glabra* var. *psychotriae* Stev. on *Psychotria grandis*, 7487, Mayaguez. On *Meliola paulliniae* Stev. on *Casearia arborea*, 5709, Monte de Oro; on *Casearia sylvestris*, 1051, Mayaguez, 7285, Arecibo-Lares Road.

Helminthosporium panici, sp. nov.—Mycelium fine, pale, in loose network. Conidiophores 170×4 μ, dark, pale at tip. Conidia 3-septate, terminal cells usually pale, central cells darker, basal cell truncate, apical cell constituting a short beak.

On *Meliola panici* E. on *Olyra latifolia*, 9159 (type), 7390, Mayaguez. On *Meliola rectangularis* Stev. on *Coccolobis laurifolia*, 7292, Arecibo-Lares Road.

Helminthosporium parathesicolum, sp. nov. (fig. 12).—Mycelium copious, fine, 1.5 μ. Conidiophores solitary, pale, 120×4 μ. Conidia 1–3-septate, 17–20×4–6 μ, base truncate, apex beaked, beak often 7 μ long.

On *Meliola parathesicola* Stev. on *Parathesis serrulata*, 8192, Las Marias (type), 7286, Arecibo-Lares Road. On *Meliola bicornis* Wint. on *Dalbergia monetaria*, Arecibo-Lares Road, 7243. On *Meliola rectangularis* Stev. on *Banisteria laurifolia*, 4392, 4384, Utuado, 7358, Hormigueros, 7564, Mayaguez.

This species is similar to *H. panici*, but is distinguished from it by the beaked conidia. It appears to be identical with the structures described as conidia of *M. bicornis* by GAILLARD, although the conidia here are somewhat smaller.

Helminthosporium philodendri, sp. nov. (fig. 13).—Mycelium fine, pale. Conidiophores abundant, long, slender, 400×3–4 μ, torulose at tip. Conidia 3-septate when mature, clavate, distinctly beaked, 24–35×5–8 μ.

On *Meliola philodendri* Stev. on *Philodendrum krebsii*, 4346, Ponce.

Helminthosporium helleri, sp. nov. (figs. 14, 15).—Mycelium fine. Conidiophores solitary, black, 230×7 μ. Conidia 3-septate when mature, clavate, 24–35×5–9 μ, well differentiated basal and apical cells.

On *Meliola helleri* E. on *Myrcia deflexa*, 8268 (type), 8296, El Alto de la Bandera; on *Eugenia stahlii*, 5343, Luquillo Forest, 8436, Jajome Alto. On

Meliola gaillardiana Stev. on *Piper aduncum*, 7794, Rio Arecibo. On *Meliola glabroides* Stev. on *Nectandra patens*, 8874, Maricao. On *Meliola thouiniae* on *Winterana canella*, 8548, 9075, Guayanilla. On *Meliola gymnanthicola* Stev. on *Gymnanthes lucida*, 8596, Guayanilla. On *Meliola toruloidea* Stev. on *Cassia quinquadrangulata*, 4015, Aibonito; on *Spondias mombin*, 749, Maricao. The short, plump, 3-septate conidia are often the most numerous types on this host. On *Meliola paulliniae* Stev. on *Paullinia pinnata*, 576, Vega Baja. On *Meliola myrsinacearum* Stev. on *Ardisia guadalupensis*, 7576, 7057, Mayaguez, 3681, 8905, Maricao. The form described as conidia of *M. pulveracea* perhaps belongs here. On *Meliola guignardi* Gaill. on *Turpinia panniculata*, 3635, Maricao. On *Meliola dipholidis* Stev. on *Dipholis salicifolia*, 8549, Guayanilla. On *Meliola monensis* Stev. on *Amyris elemifera*, 6150, Mona Island. On *Meliola furcata* Lev. on *Thrinax ponceana*, 8590, 8017, Guayanilla. This last number often shows large variation in size of spores, some being very small. On *Meliola guareae* Speg. on *Guarea trichilioides*, 7464, Mayaguez. I would place here also the forms described as conidia of *M. palmicola* Gaillard, also perhaps those of *M. patouillardi*.

Species indeterminate.—On *Meliola mayaguesiana* Stev. on *Palicourea crocea*, 7196, Lajas. Mycelium very scant, conidiophores few and scattered. Conidia not seen.

In addition to the species mentioned, other species which have been recorded on *Meliola* are *H. podosporiopsis* Pat. and *H. argentinum* Speg., both of which are 4-septate; the first on unknown host, the latter on *M. argentina* and *M. uvariae*.

Species of *Helminthosporium* which do not agree with any yet mentioned have been described as conidial stages of the following: *M. manosensis*, *M. martiniana*, *M. evodiae*, *M. hyalospora*, *M. quercinopsis*.

Sterile mycelium, probably that of *Helminthosporium*, has been recorded on *M. tomentosa*, *M. lanosa*, *M. clandestina*, *M. zig-zag*.

The "conidial stages" on *M. substenospora*, *M. quericina*, *M. anomala*, *M. butleri*, *M. pulveracea*, *M. iquitosensis*, *M. psidii*, *M. monilispora*, have been so briefly described that they are not recognizable.

On the following species of *Meliola* the species of *Helminthosporium* are perhaps distinct from those already mentioned: *M. wrightii*, *M. cryptocarpa*, *M. mitchellae*.

Isthmospora, gen. nov.—Mycelium and conidiophores dark. Conidia consisting of two approximately equal halves connected by a narrow isthmus, dark. The type of the genus is *I. spinosa.*

The species here characterized are of very unique form. They clearly belong to the Fungi Imperfecti, Dematiaceae, and in this family can only find kinship in that heterogeneous group the Staurosporae, among which, however, there is no genus closely related to the present forms. They differ from *Desmidiospora*, which has two conidial forms and a hyaline mycelium, in the absence of both of these characters. There is some resemblance to *Spegazzinia* and *Tetracoccosporium*, which have been placed in the Tuberculariaceae. The difference in spore structure, however, is sufficient to separate the genus *Isthmospora* from both of these.

Isthmospora spinosa, sp. nov. (fig. 17).—Mycelium fine, 1–2 μ, pale brown, aggregated into dense knots enveloping parts of the host mycelium. Conidiophores short, but slightly differentiated from the mycelium. The spores viewed from above are seen to consist of 4 major cells which are dark colored and rather thickly set with spines, each spine about 1 μ long. The major cells are arranged in two pairs which are connected by a 2-celled isthmus. This isthmus is flanked on either side by a circular, hyaline cell. Dimensions: total length 17–24 μ, breadth 14–20 μ, isthmus 3–4 μ wide, hyaline cell 3–4 μ in diameter.

On *Meliola psidii* Fr. on *Psidium guajava*, 3120 (type), Yauco, 5642a, Jajome Alto. On *Meliola chiococcae* Stev. on *Chiococca alba*, 7743, Vega Baja. On *Meliola byrsonimae* Stev. on *Byrsonima lucida*, 3541, Guayanilla. On *Meliola smilacis* Stev. on *Smilax coriaceae*, 5261, Manati. On *Meliola helleri* E. on *Myrcia splendens*, 5646, Jajome Alto. On *Meliola praetervisa* Gaill. on *Coccolobis sintenisii*, 7066, Mayaguez, and on *Coccolobis pyrifolia*, 7065, Mayaguez. On *Meliola philodendri* Stev. on *Philodendron krebsii*, 7225, Arecibo-Lares Road, 8994, Maricao, 4346, Ponce, 8712, El Alto de la Bandera.

Isthmospora glabra, sp. nov. (fig. 18).—Mycelium fine, 1–2 μ, pale, aggregated into knots on the host mycelium. Conidiophores short, slightly different from the mycelium. Spores of 4 major cells in 2 pairs connected by an isthmus; isthmus dark, major cells pale straw to wine colored, glabrous; total dimensions 9 × 10 μ.

On *Meliola melastomacearum* Speg. on *Clidemia hirta*, 9479, near Utuado. On *Meliola psychotriae* E. on *Gonzalagunia spicata*, 7793, Rio Arecibo, 7044, 7046, Mayaguez. On *Meliola bicornis* Wint. on *Meibomia supina*, 8975, Maricao. On *Meliola glabroides* Stev. on *Nectandra patens*, 8973, Maricao, and on

Simaruba tulae, 7588, Mayaguez. On *Meliola glabra* B. and C. (Rabenhorst. Fungi Europaei, no. 3849).

This species is clearly separated from the last by its small, irregular, pale spores, but most strikingly by the absence of spines which are so conspicuous on *I. spinosa*.

While the species have been seen only upon the recorded hosts, they may well occur upon others, since when sparsely present they are easily overlooked.

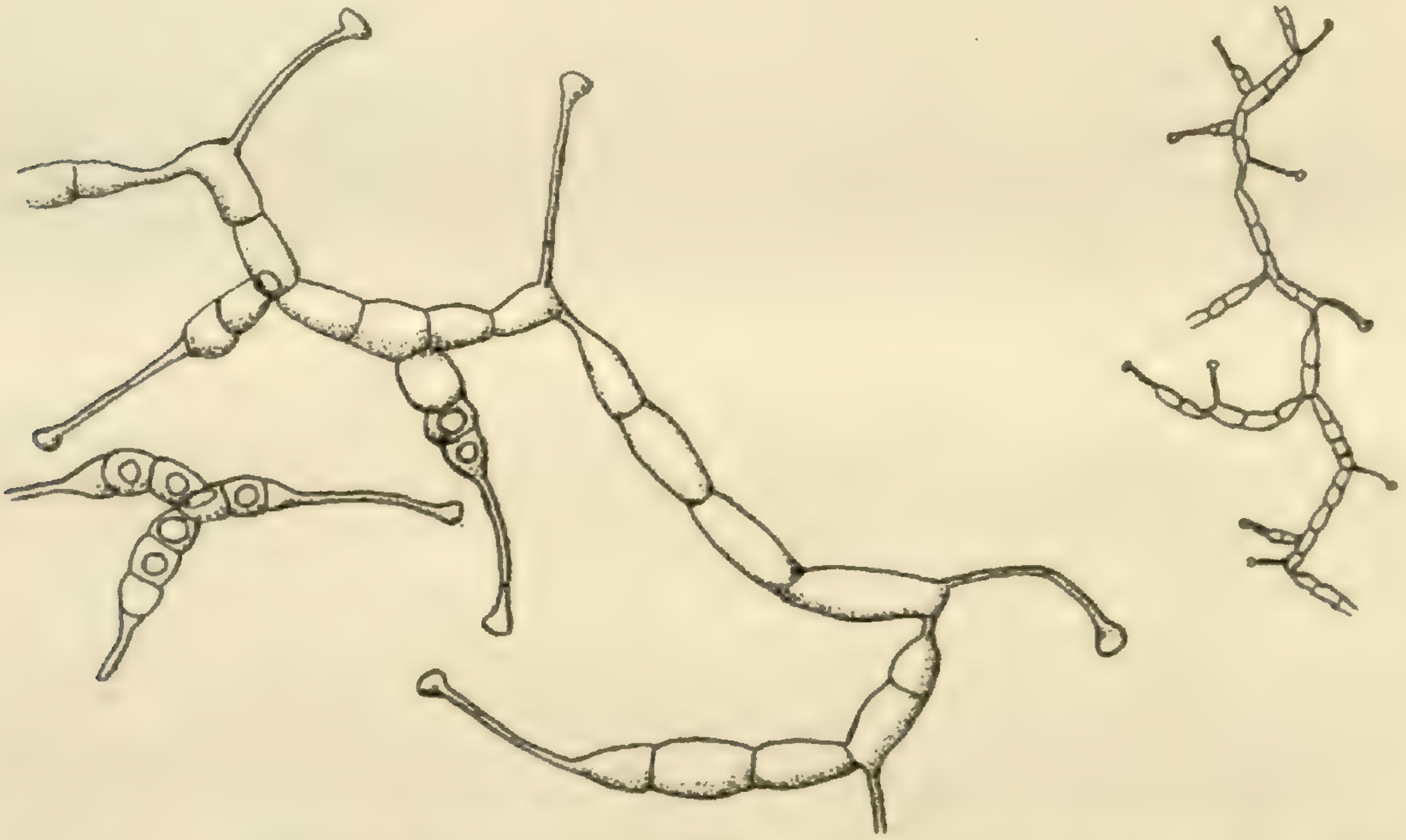

FIG. 5.—*Grallomyces portoricensis*, showing general habit of branching of mycelium and structure of supporting organs; on *Clusia minor*, no. 8283 (type) *l.p.* and *h.p.*

Fusarium meliolicolum, sp. nov.—Mycelium indistinguishable from that of *Nectria meliolicola*. Conidiophores short, cespitose in small sporodochia, 50–60 μ in diameter or by coalesence larger. Conidia clavate, curved, apex obtuse, base attenuate, 16–19 × 2.5 μ, 1–3-septate. Associated with and probably the conidial form of *Nectria meliolicola*.

On *Meliola paulliniae* on *Casearia sylvestris*, 1051, Mayaguez (type).

Grallomyces, gen. nov.—Mycelium raised from the surface by supports (*grallae*, stilts).

Grallomyces portoricensis, sp. nov. (text fig. 5).—Mycelium composed of segments arranged in zigzag fashion, strongly

constricted between segments. Supports to mycelium 17–27 μ long, with disk-formed attachments at base.

On *Clusia minor*, 8283 (type), El Alto de la Bandera; on *Guarea trichilioides*, 8166, Las Marias; on *Casearia* sp., 7074, Mayaguez; on *Mammea americana*, 8207, Las Marias; on *Palicourea crocea*, 7196, Lajas; on *Scleria* spp., 5252, Manati; on *Eugenia stahlii*, 5343, Luquillo Forest; on *Nectandra patens*, 7081, Mayaguez; on (?), 4521; on *Myrcia* sp., 818, Maricao.

The mycelium is dark brown, with some cells pale brown to straw color. It may be described as consisting of links composed of usually 4 or 5 cells each. There is some constriction at the septa between cells. The links are arranged at angles, giving the whole mycelium a zigzag or "rail fence" appearance. Each end of each link is constricted to a short (3–7 μ), narrow (2–3 μ) isthmus which forms connection with the next link. This structure is in itself remarkable enough, but more remarkable is the fact that the whole mycelium is supported free from its underlying medium by a series of "stilts" which are about 17–27 μ long. These stilts are quite uniformly distributed, one at each constriction of the mycelium, and they appear to be a projection of the constricted portion, while the next link appears as a side growth from it. The stilts are terminated by a circular enlargement which is evidently a holdfast organ. No spores or conidiophores were seen.

This fungus is often associated with *Meliola* of various species, but seems to have no connection with them. It appears to have no definite hosts, but to grow on any leaf where suitable atmospheric conditions obtain.

The following fungi not already mentioned have also been reported upon *Meliola: Dimerosporium apertum, Dimerium guinier, Hyaloderma piliferum, H. subastomum, H. tricholomum, H. lateritium, Zukalia vagans, Pseudomeliola* (?) *collapsa, Melanopsamma parasitica, Acerbiella violacea, Nectria aureola, N. bakeri, Calonectria inconspicua, C. lagerheimiana, C. erysiphoides, Paranectria wildemaniana, Lochnospermella tetraspora, Monosporium meliolicola, Mycogone meliolarum, Helminthosporium podosporiopsis, Arthrosporium parasiticum, Isariopsis penicillata, Podosporium densum, P. penicillioides, P. penicillium. Spegazzinia meliolicola, S. meliolae, S. coffeae.*

ALPHABETICAL LIST OF MELIOLAS AND THE FUNGI FOUND UPON THEM

M. ambigua.—Arthrobotryum caudatum.
M. andirae.—Calonectria graminicola.
M. arecibensis.—Coniothyrium glabroides.

M. bicornis.—Dimerium piceum, Microthyriaceae indet., Calonectria melioloides, Arthrobotryum caudatum, Helminthosporium parathesicolum, Isthmospora glabra.
M. byrsonimae.—Isthmospora spinosa.
M. chiococcae.—Belonidium leucorrhodinum, Isthmospora spinosa.
M. comocladiae.—Helminthosporium glabroides.
M. compositarum.—Coniothyrium glabroides.
M. compositarum var. portoricensis.—Perisporium meliolae, Dimerium piceum, Calonectria melioloides, Coniothyrium glabroides, Helminthosporium glabroides.
M. cupaniae.—Calonectria melioloides.
M. didymopanicis.—Arthrobotryum caudatum, Helminthosporium glabroides.
M. dieffenbachiae.—Arthrobotryum dieffenbachiae.
M. dipholidis.—Helminthosporium helleri.
M. furcata.—Helminthosporium helleri.
M. gaillardiana.—Microthyriaceae indet., Helminthosporium glabroides, H. helleri.
M. gesneriae.—Helminthosporium glabroides.
M. glabra.—Isthmospora glabra.
M. glabra var. psychotriae.—Dimerium piceum, Microthyriaceae indet., Arthrobotryum caudatum, Helminthosporium melastomacearum.
M. glabroides.—Dimerium piceum, Microthyriaceae indet., Paranectria meliolicola, Coniothyrium glabroides, Arthrobotyrum glabroides, A. caudatum, Helminthosporium glabroides, H. helleri, Isthmospora glabra.
M. guareae.—Helminthosporium helleri.
M. guareicola.—Coniothyrium glabroides, Helminthosporium glabroides.
M. guignardi.—Helminthosporium helleri.
M. gymnanthicola.—Helminthosporium helleri.
M. helleri.—Microthyriaceae indet., Helminthosporium helleri, Isthmospora spinosa.
M. hessii.—Perisporium paulliniae, Calonectria melioloides, Helminthosporium glabroides.
M. hyptidicola.—Microthyriaceae indet., Naemosphaera hyptidicola, Arthrobotryum caudatum.
M. ipomoeae.—Dimerium piceum.
M. longipoda.—Microthyriaceae indet., Arthrobotryum caudatum, Helminthosporium glabroides.
M. maricaensis.—Helminthosporium glabroides.
M. mayaguesiana.—Helminthosporium helleri.
M. melastomacearum.—Microthyriaceae indet., Nectria portoricensis, Arthrobotryum caudatum, Helminthosporium ocoteae, Isthmospora glabra.
M. monensis.—Calonectria melioloides, Helminthosporium helleri.
M. myrsinacearum.—Helminthosporium helleri.

M. nigra.—Helminthosporium glabroides.
M. ocoteae.—Helminthosporium ocoteae.
M. panici.—Dimerium piceum, Calonectria graminicola, Coniothyrum glabroides, Arthrobotryum penicillium, Helminthosporium panici.
M. parathesicola.—Helminthosporium parathesicolum.
M. philodendri.—Helminthosporium philodendri, Isthmospora spinosa.
M. praetervisa.—Isthmospora spinosa.
M. paulliniae.—Dimerium piceum, Nectria meliolicola, Calonectria melioloides, Arthrobotryum caudatum, Helminthosporium melastomacearum, H. helleri, Fusarium meliolicolum.
M. psidii.—Isthmospora spinosa.
M. psychotriae.—Microthyriaceae indet., Arthrobotryum caudatum, Helminthosporium glabroides, Isthmospora glabra.
M. pteridicola.—Dimerium piceum, Microthyriaceae indet., Coniothyrium glabroides, Arthrobotryum caudatum, Helminthosporium glabroides.
M. puiggiarii.—Helminthosporium glabroides.
M. rectangularis.—Nectria portoricensis, Helminthosporium panici, H. parathesicolum.
M. rudolphiae.—Belonidium leucorrhodinum.
M. smilacis.—Isthmospora spinosa.
M. thouiniae.—Helminthosporium helleri.
M. tortuosa.—Belonidium leucorrhodinum, Dimerium piceum, Pseudonectria pipericola, Calonectria melioloides, Paranectria meliolicola, Coniothyrium glabroides.
M. toruloidea.—Calonectria graminicola, Helminthosporium glabroides, H. helleri.
M. triumfettae.—Microthyriaceae indet.
Microthyriaceous fungus.—Paranectria miconiae.

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EXPLANATION OF PLATES V AND VI

(*l.p.* indicates low power; *h.p.*, high power)

PLATE V

Arthrobotryum

FIG. 1.—*A. glabroides:* fine mycelium overgrowing coarse mycelium of *Meliola;* 7595a, *l.p.*

FIG. 2.—Same, *h.p.*

FIG. 3.—Spores: 7595b, *h.p.*

FIG. 4.—*A. dieffenbachiae:* coremium on a seta; 8077, setal forkings are clearly shown in the coremium.

STEVENS on MELIOLA PARASITES

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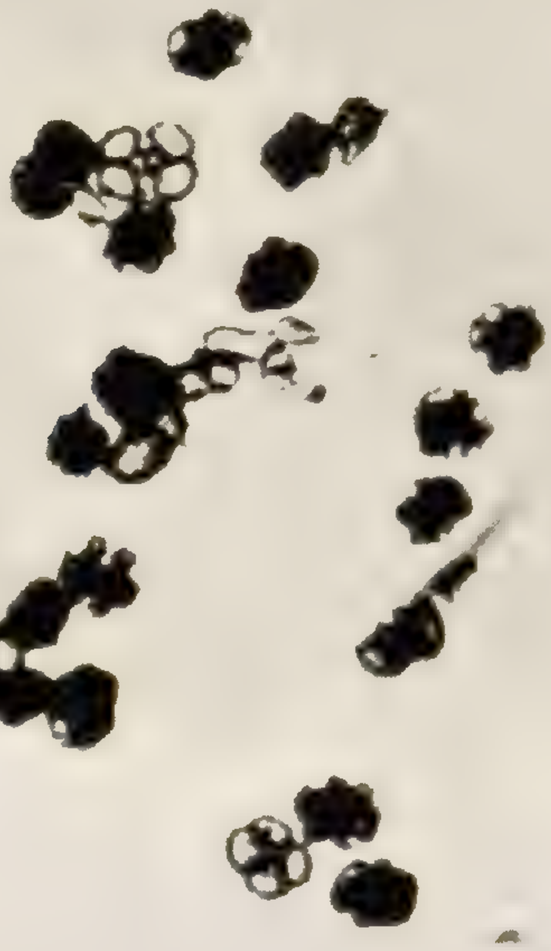

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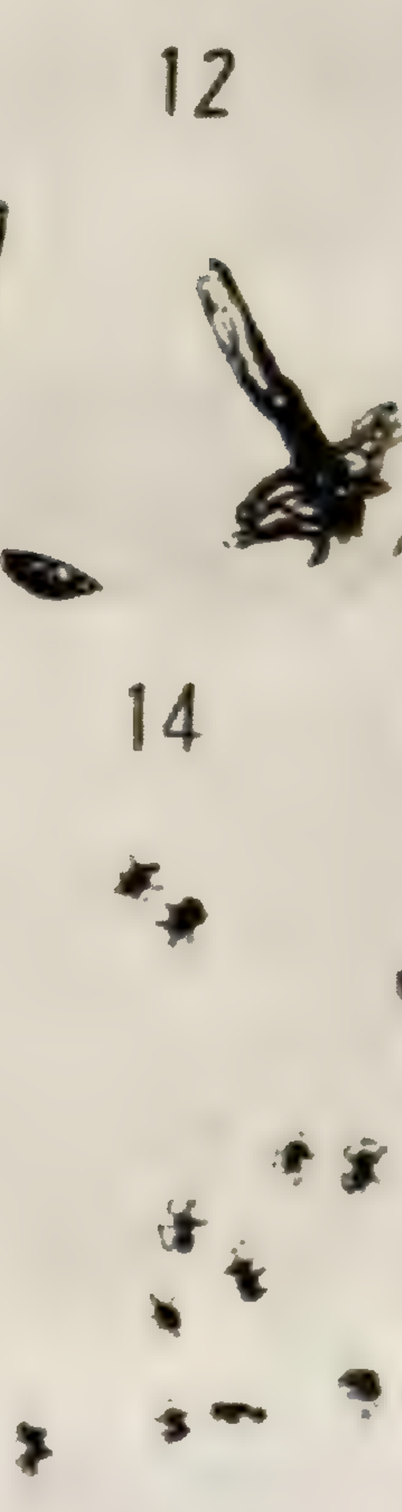

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STEVENS on MELIOLA PARASITES

FIG. 5.—*A. caudatum*, showing coremia; *l.p.*
FIG. 6.—*A. caudatum*, showing 2 kinds of mycelium and spores; 7745.
FIG. 7.—*A. caudatum*, showing coremia; 468, *l.p.*

Helminthosporium

FIG. 8.—*H. glabroides* on *Meliola polytricha:* conidia; 1256, Kew Botanical Gardens, *h.p.*

PLATE VI

FIG. 9.—*H. glabroides:* typical long and short spores; 9039, *h.p.*
FIG. 10.—*H. glabroides* on *M. longipoda:* conidia on conidiophores, showing that truncate end is basal; 7965, *h.p.*
FIG. 11.—*H. melastomacearum* on *M. melastomacearum:* conidia and conidiophores; 7389, *l.p.*
FIG. 12.—*H. parathesicolum* on *M. parathesicola:* spores; 8192, *h.p.*
FIG. 13.—*H. philodendri* on *M. philodendri:* spores; 4346, *h.p.*
FIG. 14.—*H. helleri* on *M. helleri:* spores and a conidiophore showing its mycelium; 8268, *h.p.*
FIG. 15.—*H. helleri* on *M. guignardia:* spore; 3635, *h.p.*
FIG. 16.—*H. guareicolum* on *M. guareicola:* 8166, *h.p.*, showing toruloid conidiophores.

Isthmospora

FIG. 17.—*I. spinosa:* spores; 3120, *h.p.*
FIG. 18.—*I. glabra:* spores; 9479, *h.p.*

ANATOMY OF CERTAIN GOLDENRODS[1]

EDITH S. WHITAKER

(WITH PLATES VII AND VIII AND ONE FIGURE)

In dealing with the anatomical features of *Solidago*, and especially in studying the modifications of its woody cylinder in relation to the leaf trace, it is well to bear in mind the fact that the goldenrods belong to a family which occupies a high place systematically. The largest proportion of herbs and short-lived perennials, especially in temperate regions, belongs to the Compositae; and since they are so generally admitted to be high forms, a certain amount of evolutionary progress can be taken for granted in studying them. Another advantage in investigating genera of the Compositae is the fact that in the family and in any genus of the family both the woody and herbaceous type of stem may be found; hence comparisons are more easily made and conclusions more readily drawn. Not only within the same genus are both kinds of stem to be found, but the same aerial axis has regions which are characteristically woody and herbaceous. This situation is well illustrated by *Solidago*. In the lower portions of the aerial axis, as well as in the subterranean parts of the stem, the organization is typically woody; while in the higher and more slender portions of the stem the herbaceous type prevails. In short, *Solidago* presents an epitome of a woody-herbaceous condition in which the transition from one type to the other is advantageously elucidated.

The species of goldenrod studied were *Solidago canadensis*, *S. bicolor*, *S. rigida*, *S. caesia*, *S. speciosa*, *S. sempervirens*, *S. graminifolia*, *S. latifolia*, *S. serotina*, and *S. patula*. It was found that in all these species there are certain modifications of the woody cylinder related definitely to the leaf strands. These consist in the transformation of portions of the woody segment through which the leaf trace takes its departure into parenchyma and in the elimination of fibers and vessels.

[1] Contributions from the Laboratories of Plant Morphology of Harvard University.

There are, as a rule, three traces to each leaf in *Solidago*, a median and two laterals. In some species (for example, *S. rigida*, *S. patula*, and *S. sempervirens*) there is a multiplication of traces, correlated apparently with the increased size and vigor of the plants and especially with the size of their leaves. The species mentioned, besides being very large and leafy, are characterized by having large, full heads of flowers.

In studying the modifications of the woody cylinder, the median trace need not be especially considered, since conditions here are complicated by the presence of the axillary bud. Attention accordingly may be directed to the lateral traces, which present a simpler situation. The most conservative part of the stem is at the node; and conditions at the node, therefore, are the most significant. A section cut transversely through the node of the woody axis of any of the species of *Solidago* mentioned shows the leaf traces still in the cortex. Following the traces down in serial sections, it is to be noted that they enter the woody cylinder a short distance below the node and are surrounded on all sides by parenchyma. One leaf trace usually passes into the stele at a higher level than the others. Consequently, sections cut at different distances below the node show the traces in different topographical relations. For a considerable interval downward the trace is surrounded on all sides by parenchyma, so that the storage elements are present not only on the sides of the trace but confront it externally as well.

Fig. 1 shows a transverse section of *S. canadensis* cut far enough below the node so that only one of the lateral traces (the one on the right which entered the cylinder much lower than the corresponding trace on the left) appears surrounded on all sides by parenchyma. Figs. 2, 3, and 4 show this situation under higher degrees of magnification and in the three dimensions respectively. Fig. 2 is a high power representation of the transverse section of a lateral leaf trace segment of *S. canadensis*. The foliar strand can be seen lying at the bottom of the figure, obviously surrounded by storage parenchyma, which both confronts it radially and lies on either side of it. In this section it is clear that a portion of the cylinder opposite the leaf trace has undergone considerable modification, apparently in relation to the photosynthetic activity of the leaf. The cauline

segment in relation to it may conveniently be designated as the leaf trace segment. Fig. 3 shows the same situation in longitudinal tangential aspect. Here the trace appears high up in the center of the figure and is obviously surrounded on all sides by parenchymatous tissue. This section was made near the region of the cortex, so that it represents the leaf strand after it has become horizontally inclined. Fig. 4 is a radial view of the same situation, illustrating in a similar manner the imbedding of the leaf trace in storage tissue in its course through the woody cylinder. This section also demonstrates the fact that vessels and fibers again make their appearance in the cylinder directly above the leaf trace segment after the foliar strand has passed into the cortex.

It is clear from the foregoing illustrations that the woody cylinder opposite the leaf trace undergoes certain modifications in relation to the activity of the foliar organ. The strand as it passes upward and outward through the cylinder is flanked on either hand by storage tissue which may be designated as flanking parenchyma. Farther in its outward course, and more marked where the cylinder is thick, subtending the trace externally is a mass of tissue which may appropriately be called subtending or confronting parenchyma. Above the trace is the parenchymatous interval known as the leaf gap. It is noteworthy in this connection that the leaf trace in the thick or woody cylinder (and all the axes here figured are aerial) of *S. canadensis* has the same topographical relation to storage devices as is found in arboreal types like *Quercus*, *Casuarina*, etc. The origin and topographical relations of the broad ray in the oak have clearly and convincingly been elucidated by EAMES,[2] and the conclusions reached by this author have been shown by BAILEY[3] to hold with equal validity for the Betulaceae and Fagaceae in general. EAMES[4] has also shown that the woody type in the Rosaceae is subject to the same general modifications in relation to the leaf trace as obtained in the Betulaceae, Fagaceae, and also,

[2] EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. **49**:161–167. 1910.

[3] BAILEY, I. W., Relation of leaf-trace to compound rays in lower dicotyledons. Ann. Botany **25**:225–241. *pls. 15–17. fig. 1.* 1911.

[4] EAMES, A. J., Herbaceous type in angiosperms. Ann. Botany **25**:215–224. *pl. 14.* 1911.

as has been shown, in the woody aerial stem of *Solidago*. It is clear that there is a general agreement regarding the part the leaf trace plays in relation to the transformation of portions of the woody cylinder into a parenchymatous segment.

Concerning the comparableness of woody types like the oak, etc., with those presented by axes characteristically herbaceous, however, some doubts have been raised. It has, for instance, been maintained by SINNOTT and BAILEY[5] that the herbaceous type does not come from the woody through the conversion of secondary xylem opposite the leaf strand into storage parenchyma, but, on the contrary, that the evolution of herbaceous forms has come about through the reduction in amount of secondary wood and increase in width of the broad rays. This, together with their decrease in radial extent, has resulted in the confining of the storage tissue in herbaceous axes to the sides of the leaf trace, with the result that parenchyma in no case subtends the trace as in the oak, etc. "In practically all families of herbs, the interfascicular parenchyma is never subtended by a tiny leaf trace bundle of protoxylem, but always abuts directly on the pith tissue between the strands of primary wood" (*loc. cit.* p. 596). Hence it is assumed that the significant conditions in the woody stem in relation to the leaf trace are in no way responsible for the origin of the herbaceous form. It is further claimed, in substantiation of this hypothesis, that the condition outlined for the Betulaceae, etc., while it holds for the subterranean parts of the woody axis, does not explain the situation in the aerial region of the herbaceous stem where "the actual evolutionary development must have taken place (*loc. cit.* p. 555).

The situation in the herbaceous part of *Solidago* may be described. Fig. 5 represents a slender stem of *S. canadensis*, which is obviously herbaceous. The section was made just below the node and shows the three leaf traces at the top. At the bottom and a little to the right, the three traces of the next higher node may be seen. In the upper part of the figure, even under the comparatively low power of magnification, it can easily be noted that the

[5] SINNOTT, E. W., and BAILEY, I. W., Investigations on the phylogeny of the angiosperms. IV. The origin and dispersal of herbaceous angiosperms. Ann. Botany **28**:547–600. *pls. 39, 40.* 1914.

traces pass out surrounded by parenchyma. Fig. 6 is a more highly magnified view of one of the lateral leaf traces, showing that even in the upper aerial region of this persistently woody species confronting as well as flanking parenchyma is present. Fig. 6 also elucidates the relatively greater size of the leaf trace in proportion to the segment, as compared with fig. 2. Allowing for the difference in the size of the leaf trace and for the inevitable thinning of the cylinder in the more slender portions of this particular stem, as well as in herbaceous forms generally, one can readily see how, if the cylinder were sufficiently reduced in size, the subtending storage tissue would be confined to the sides of the foliar strand even in the region of the node. Lower in the internode there would normally be only flanking parenchyma, since the central region of the confronting parenchyma is transformed below into a characteristically woody segment composed of vessels, fibers, etc. EAMES (*loc. cit.*) has made it clear that in the Rosaceae in which both woody and herbaceous types occur the latter has undoubtedly come from the former by the parenchymatous transformation of more and more secondary wood in proximity to the leaf traces. Hence the bundles of the herbaceous stem represent ordinary woody segments interspersed with other segments which have undergone the parenchymatous metamorphosis described.

It would seem fairly clear from the preceding descriptions that the highest dicotyledons present the same general conditions of modification of the originally woody cylinder in relation to storage and the leaf trace as is found in the lower groups, such as the Betulaceae, Fagaceae, etc. It is quite clear that the herbaceous type has originated in a similar manner and largely as the result of the thinning of the woody cylinder. *Solidago* obviously illustrates this transition stage, since it shows in its herbaceous regions the same topographical relation to the cylinder as is found in the typically woody part of the axis. To elucidate this point, and chiefly for the sake of making the situation indubitably clear, the accompanying diagrams have been introduced.

In text fig. 1, *A* represents the woody portion of *Solidago*, and would also hold equally well for the woody dicotyledons with large foliar rays. On the other hand, *B* elucidates the characteristic

herbaceous condition in a dicotyledonous stem. In *A* the condition presented by figs. 2, 3, 4, and 6 is illustrated. The departing leaf traces in the region of the node, especially as they bend outward through the cylinder, are both flanked and subtended by storage parenchyma, a situation shown diagrammatically in black. *B* illustrates the topography of the herbaceous region of the stem in the Compositae, where, by reason of the greater relative importance of the leaf trace, its radial diameter nearly equals that of the ordinary xylem segments of the cylinder. As a consequence, the confronting parenchyma of *A* is conspicuously absent and the storage

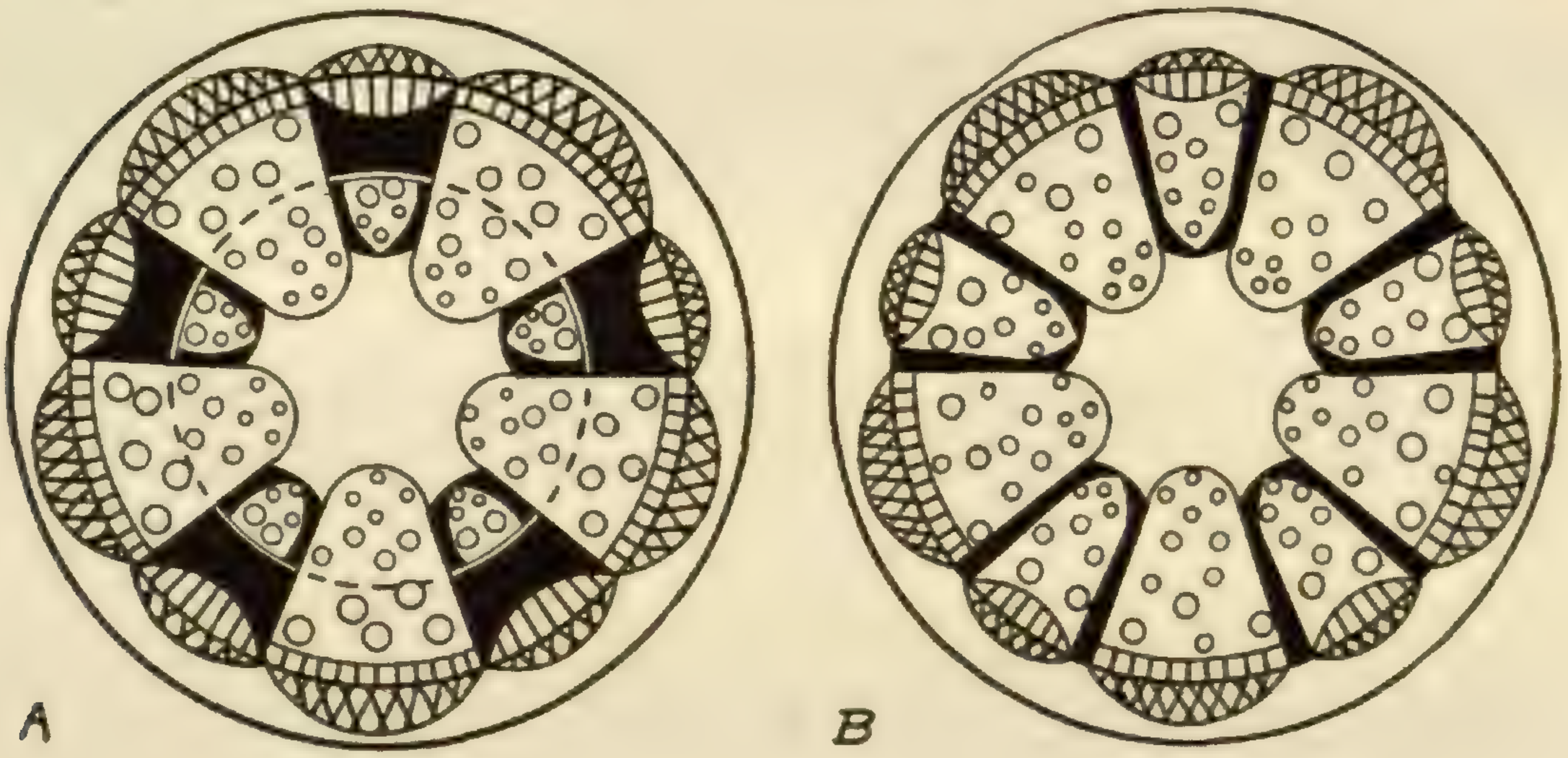

FIG. 1

tissue, as a necessary geometrical result, is confined to the flanks of the narrower segments representing the foliar strands. This exaggeration of the leaf trace in the herbaceous type is probably in response to the greater relative size and importance of the leaves. That the situation outlined in *B* obviously results from the thinning of the cylinder, with the consequent confining of the storage tissue exclusively to the sides of the trace, will be evident by referring to *A* and supposing the woody cylinder here to be considerably reduced in thickness. This hypothetical thinning of the cylinder is represented by a broken line drawn through the stele just outside the leaf traces. A comparison of the portion of the cylinder thus limited in *A* with the herbaceous type represented in *B* shows that the conditions inside the broken line are substantially the same as

those depicted in the latter illustration. The parenchyma in both is flanking only and the leaf trace plays a predominant part.

Hence, from a consideration of the situation obtaining from the lower dicotyledons to the Compositae, it would seem clear that the herbaceous type has been derived from the woody through the conversion of segments related to the outgoing leaf strand into wood parenchyma; and that in extreme herbaceous types the storage tissue has become confined to the sides of the trace by the simple process of the thinning of the cylinder and the increased relative importance of the foliar strand.

An interesting feature of some species of *Solidago* is the multiplication of leaf traces, a situation which might be expected in relation to the increased efficiency of the leaves. As has been stated, the usual number of traces in this genus is 3; but in more vigorous stems the leaf traces may be more numerous. In *S. patula*, for instance, there are 5; and in *S. sempervirens*, the salt marsh goldenrod, there are as many as 7 or 9, according to the vigor of the plant. This condition is represented in fig. 7, which is a transverse section of *S. sempervirens*. In the instances where there is a multiplication of leaf traces, it is noteworthy that in addition to stout and leafy stems, these species are likewise characterized by unusually large and full heads of flowers.

Another point of interest, which is of course a common anatomical characteristic of the Tubuliflorae, is the presence of oil canals in the pith or cortex, or in both. In fig. 7, which is a cross-section of *S. sempervirens*, these oil canals may easily be noted in both pith and cortex; and in fig. 5, which represents the same plane in *S. canadensis*, they are visible in the cortex only.

An additional feature of interest is presented by the leaf bundles in the cortex, namely, the presence of internal phloem. This is shown in fig. 8, which is a high magnification of one of the cortical bundles of *S. sempervirens*. Other species of *Solidago*, for example, *S. canadensis*, *S. patula*, *S. rigida*, etc., show the same organization of their cortical bundles, and it seems to be a general condition for the genus. It has been suggested by WORSDELL[6] in the case of the Cucurbitaceae that internal phloem is a "vestigial structure." In

[6] WORSDELL, W. C., The origin of medullary (interxylary) phloem in the stems of dicotyledons. Ann. Botany **29**: 567–590. *figs. 10.* 1915.

this family (the Cucurbitaceae), as is well known, the stem bundles are characterized by the presence of internal phloem. The conclusion has been reached by this author, as a result of the study of the conservative regions, that the internal phloem is derived from inversely oriented medullary bundles fused with the inner surface of the woody cylinder. The situation in *Solidago* (and in other genera of the Compositae) is of interest in this connection, especially as the presence of internal phloem is so constant a feature of the organization of the leaf trace in its course through the cortex. Since the results of comparative anatomical study of existing and extinct gymnosperms show clearly the conservative character of the leaf trace, it seems fairly obvious that the Compositae once possessed internal phloem in the stem like the Cucurbitaceae, Solanaceae, etc., but have lost it as a result of subsequent modifications. It may be pointed out that this assumption accords with the high systematic position ordinarily assigned to the family. This conclusion is in no way weakened by the fact that the Compositae are actually included in the same large group or cohort as the Cucurbitaceae, namely, the Campanulales (Campanulatae).

In *Solidago* and most genera of the Compositae there are depressions in the woody cylinder corresponding to the leaf trace segments. Work carried on in this laboratory by Mr. J. P. POOLE on *Helianthus* has demonstrated that in this genus the depressions invariably correspond to the foliar segment. Fig. 9, which is a woody stem of *H. hirsutus*, is inserted here because it illustrates this situation so diagrammatically. At either side two median traces are to be seen, and also their two corresponding lateral traces, making in all 6 depressions in the cylinder and 6 corresponding parenchymatous modifications. Most species of *Solidago* show similar depressions in immediate relation to the foliar segment. BAILEY[7] has made it clear that in the oak these depressed segments are caused by the retarding influence on growth of pairs of closely approximated compound foliar rays. The depressions in the Compositae in relation to the leaf trace segments are likewise connected with growth mechanics.

[7] BAILEY, I. W., The evolutionary history of the foliar ray. Ann. Botany **26**: 647–661. *pls. 62–63.* 1911.

The situation in the oak, however, is somewhat different from that outlined for *Helianthus* and the Compositae generally; for in the oak the depressions are xylem segments *between* the lateral compound leaf rays and do not correspond to the leaf trace segment itself as in the Compositae. For purposes of elucidation the situation presented by the oaks may be briefly reviewed. In *Quercus* the two predominant lateral traces of each foliar organ are related to foliar rays which are typically in 5 pairs, corresponding to the two-fifths phyllotaxy of the oak. Between these approximated pairs of rays there is a "dipping in" of the cylinder as a consequence of the retarding influence on growth of the rays in question.

In some genera of the Compositae we get a situation approximating that in the oaks, and as a result contrasting with that figured for the sunflower, etc., in fig. 9. In *S. graminifolia*, for instance, the depressions do not correspond to single leaf trace segments as is usual in the Compositae, but are in relation to the xylem segments between the leaf rays. This situation may be noted in fig. 10, a section of *S. graminifolia* cut in the region of the node. The result of the depression of segments between the rays is that the stem is roughly divided into 5 parts as in the oak. The pith is 5-angled and the median trace comes off opposite an angle of the pith precisely as in *Quercus*. Fig. 11 shows a portion of the same more highly magnified, illustrating how striking is the depression and how clear the analogy to the oak. Fig. 12, which at first sight might easily be taken for a section of an oak twig, is really a transverse section of *Aster multiflorus*, and elucidates this phenomenon even more strikingly. Here there can be no doubt that the depressions in the cylinder occur between pairs of rays exactly as in *Quercus*, and do not correspond to single leaf trace segments. This topographical condition of the stem is rare in the Compositae, although it is occasionally present in *Solidago*, as for example in *S. graminifolia*, and is extremely common in the genus *Aster*.

Summary and conclusion

Solidago is a genus which occupies a very high place systematically and presents both woody and herbaceous types of stem, not only in the genus but also in different regions of the axis of the same species. The modifications of the stem, especially the transition

from one type to the other, therefore, can be studied to good advantage in this and other genera of the Compositae.

In connection with the derivation of the herbaceous type it has been shown that the general principles derived from the study of the Betulaceae, Fagaceae, Rosaceae, etc., hold equally well for this particular genus of the Compositae. Here as there the same storage modifications result from the transformation of woody tissues surrounding the outgoing leaf traces. No vessels appear in the leaf trace segment in the region just below the node, but at a lower level in the internode the foliar segment again becomes woody with typical vessels and fibers.

In the slender herbaceous part of the aerial axis the same general situation obtains. The traces, however, are relatively well developed in proportion to the size of the segment, and the cylinder as a whole is thinner. This thinning of the cylinder automatically results in the limiting of the storage elements to the flanks of the foliar strands in extreme herbs.

It seems noteworthy that in some species of *Solidago*, for example, in *S. sempervirens*, but occurring also in other species, there is a multiplication of the foliar traces which seems to be definitely correlated on the one hand with greater vegetative vigor and on the other hand with more numerous and larger heads of flowers.

Internal phloem in the leaf bundles of the cortex is a general feature of the genus and probably of the family. It seemingly perpetuates a condition which was once characteristic of the bundles of the axis.

Solidago occasionally resembles the oak anatomically by the "dipping in" of woody segments between the leaf rays in contrast to depressions in the cylinder corresponding to single leaf trace segments, as in *Helianthus* and the Compositae generally. The depression of the cylinder between leaf rays is the usual situation in the genus *Aster*, which, with certain species of *Solidago*, are exceptions to the general rule for the Compositae.

In conclusion I wish to thank Dr. E. C. JEFFREY, under whose direction this investigation has been carried on, for material, valuable advice, and suggestions.

HARVARD UNIVERSITY

EXPLANATION OF PLATES VII AND VIII

FIG. 1.—Transverse section of woody stem of *Solidago canadensis;* ×10.

FIG. 2.—Lateral leaf trace segment of same more highly magnified; ×50.

FIG. 3.—Tangential view of same; ×60.

FIG. 4.—Radial view of same; ×60.

FIG. 5.—Transverse section of upper and more herbaceous region of *S. canadensis;* ×15.

FIG. 6.—Lateral leaf trace segment of same more highly magnified; ×120.

FIG. 7.—Transverse view of section of *S. sempervirens* showing multiplication of leaf traces; ×12.

FIG. 8.—Leaf trace bundle of same section more highly magnified; ×150.

FIG. 9.—Transverse section of woody stem of *Helianthus hirsutus;* ×10.

FIG. 10.—Transverse section of *S. graminifolia;* ×8.

FIG. 11.—Part of thinner cylinder of same species more highly magnified; ×40.

FIG. 12.—Transverse view of section of *Aster multiflorus;* ×12.

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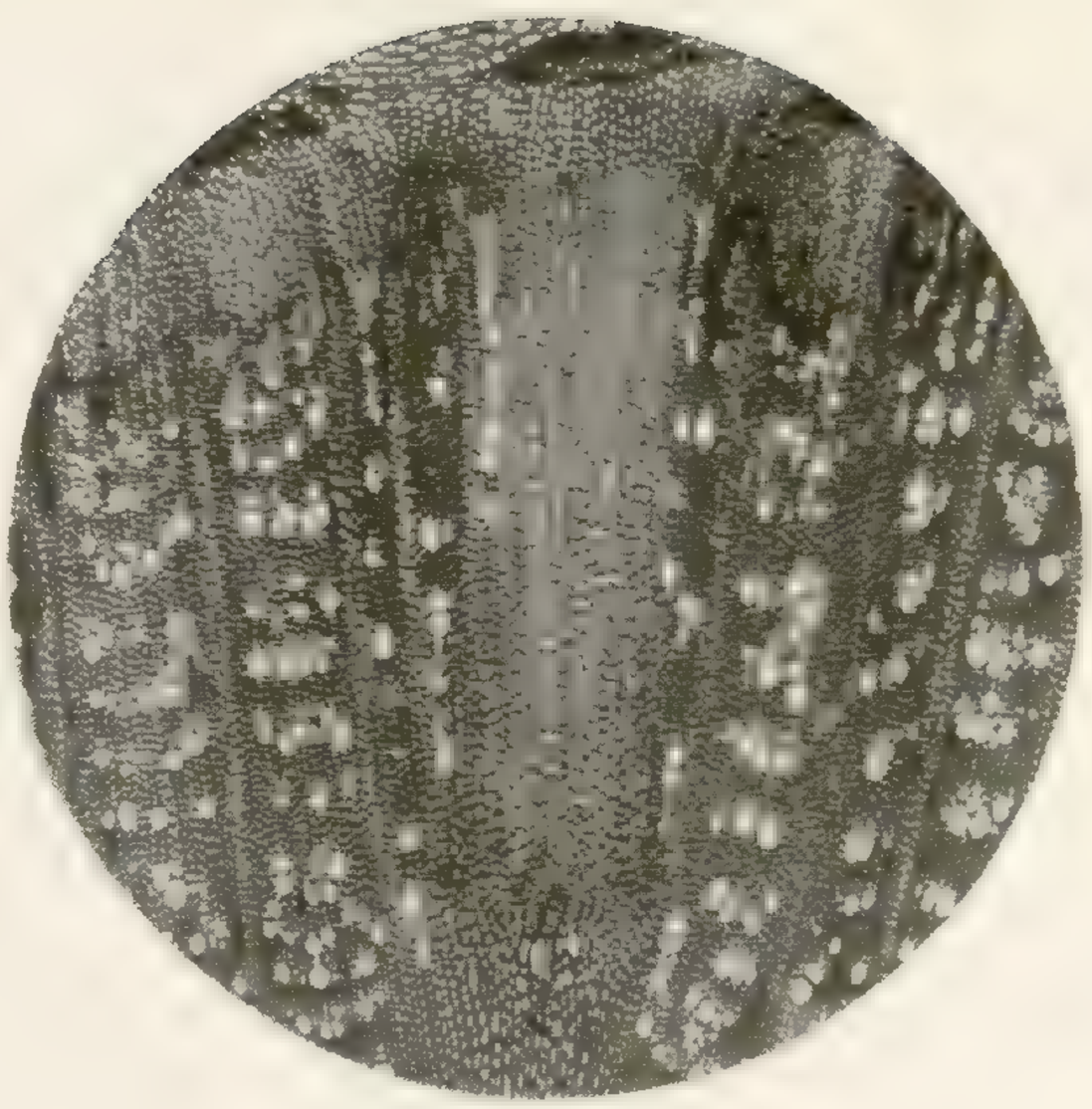

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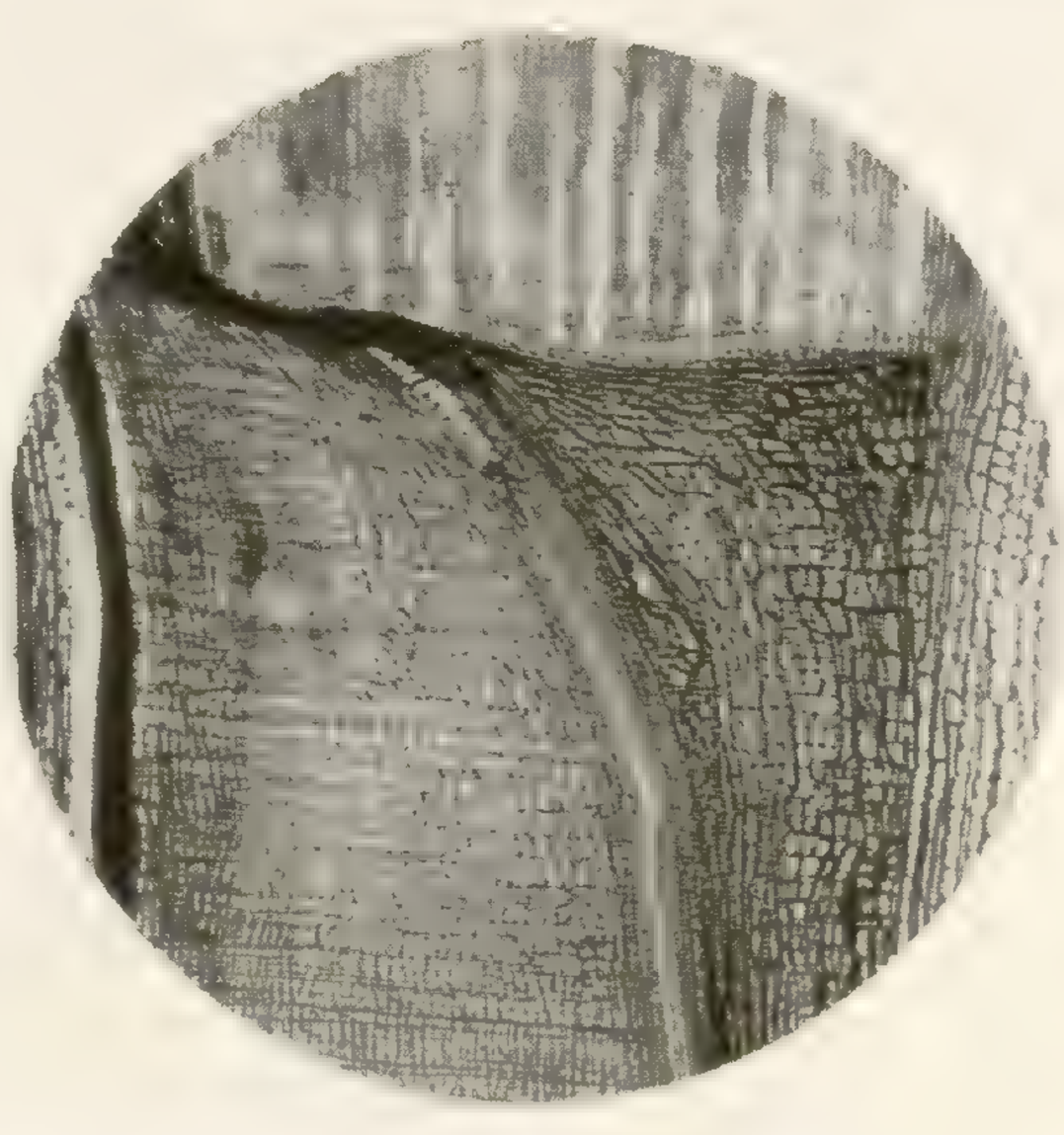

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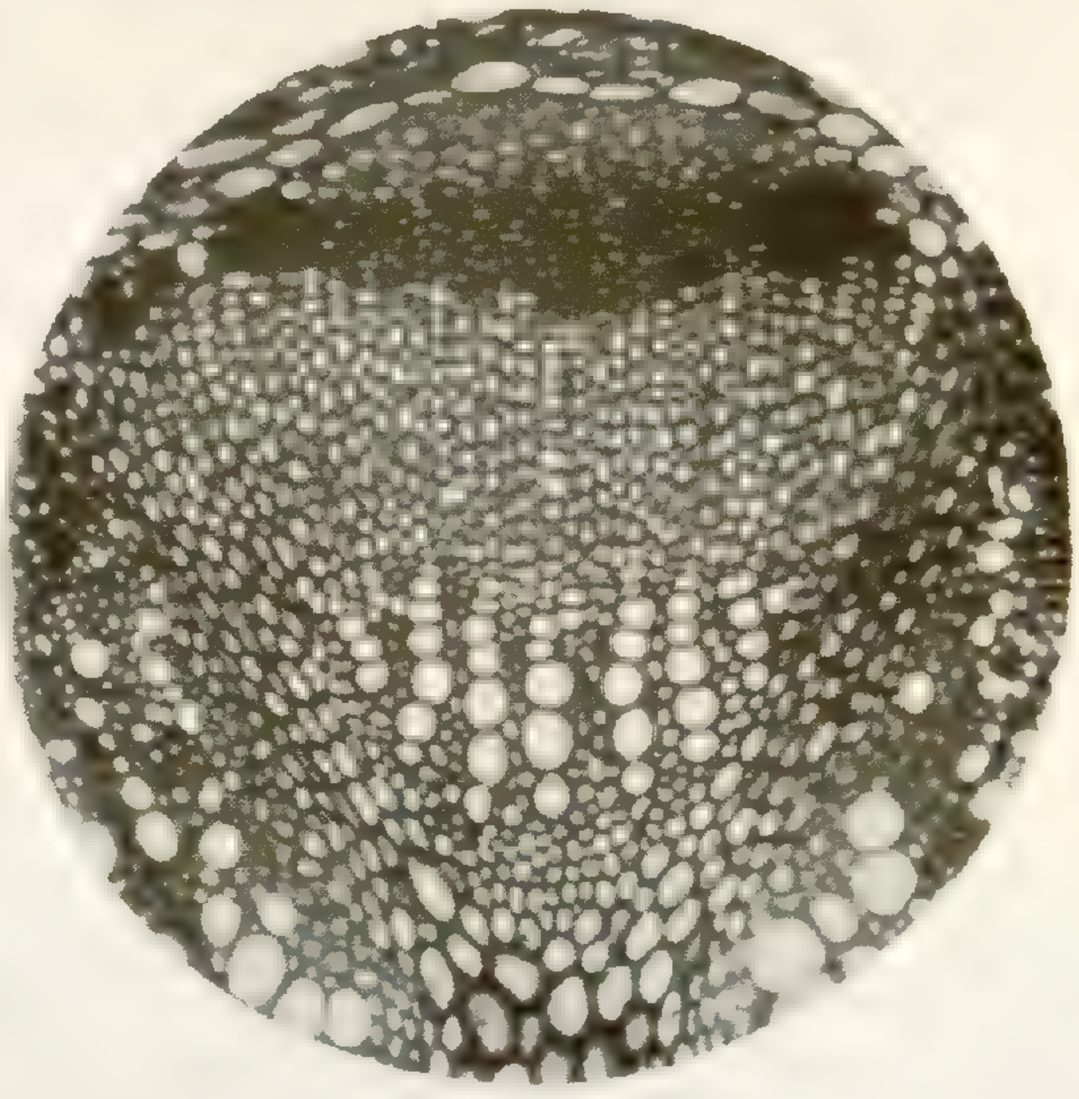

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WHITAKER on SOLIDAGO

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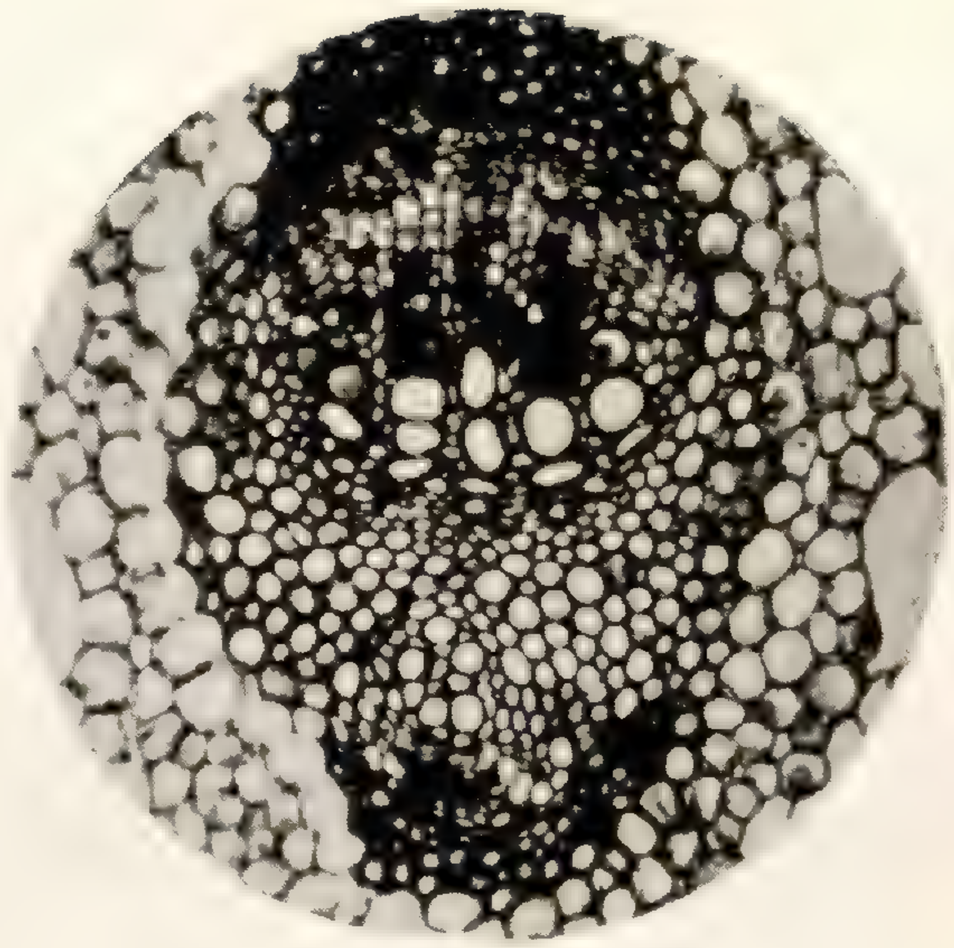

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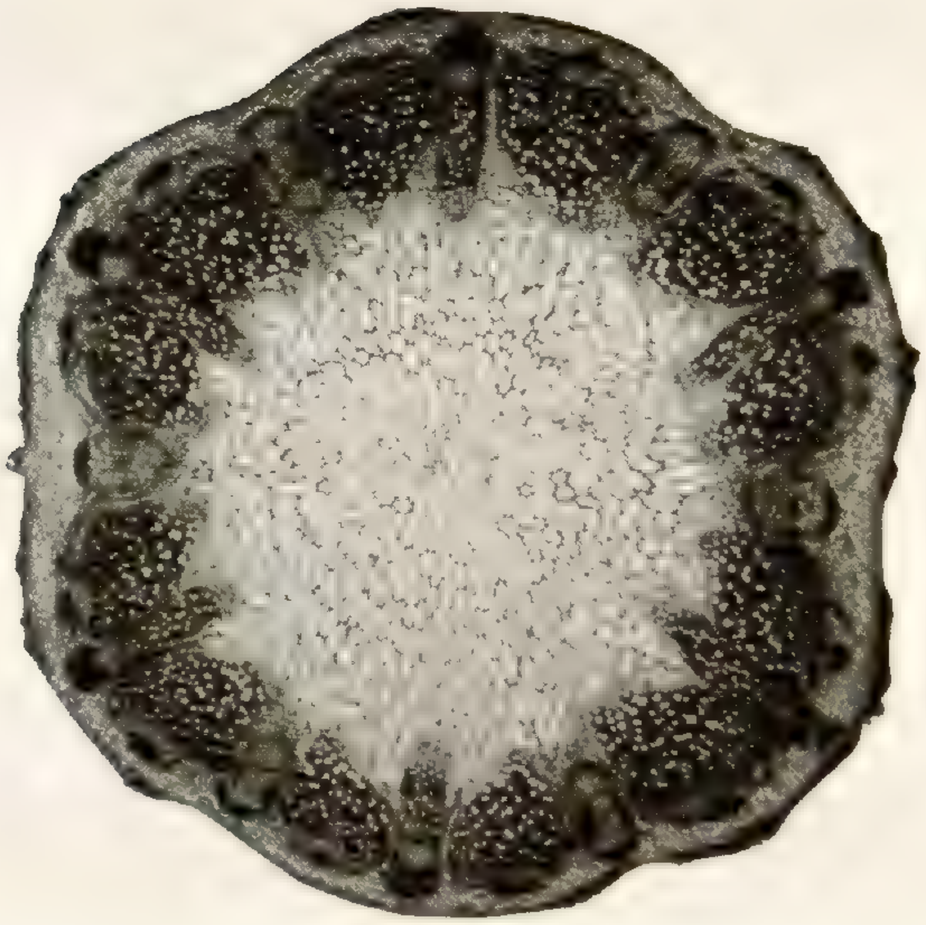

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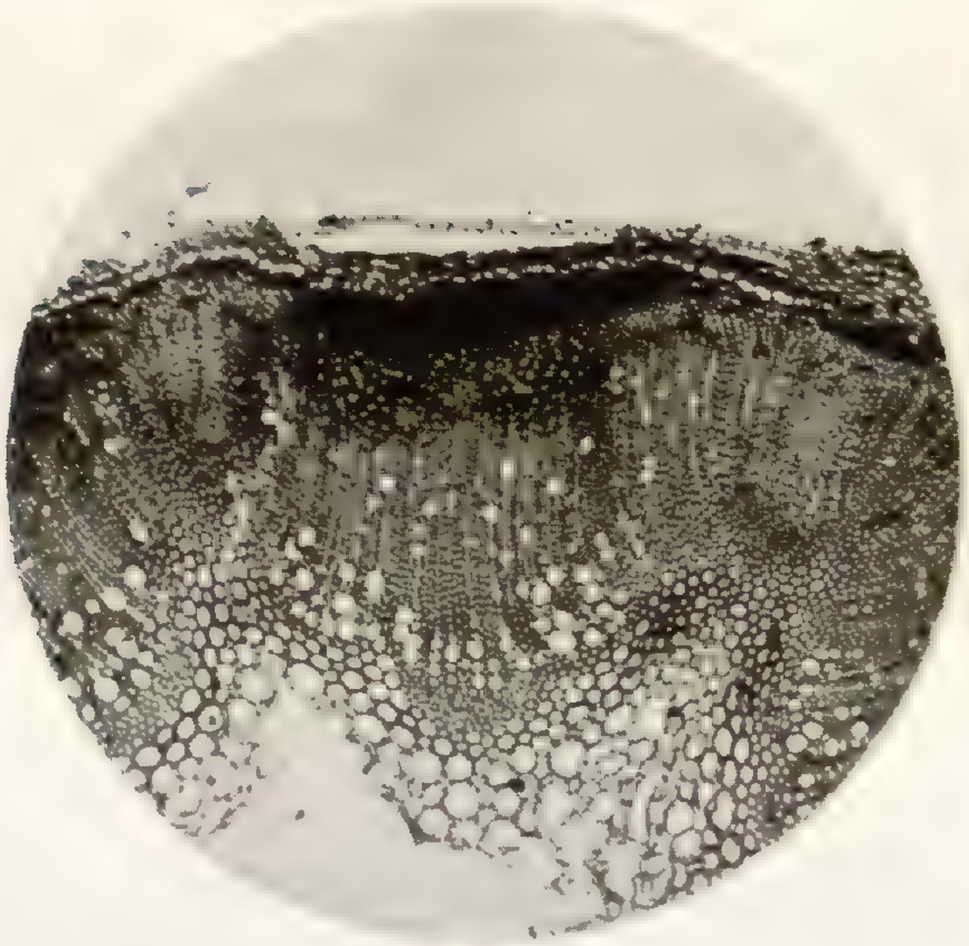

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WHITAKER on SOLIDAGO

PELEA AND PLATYDESMA

JOSEPH F. ROCK

(WITH ONE FIGURE)

The family Rutaceae is represented in the Hawaiian Islands by several genera, of which the genus *Pelea*, named by ASA GRAY after the Hawaiian goddess of fire Pele, is the largest. The species, which number about 30, including the two here described, are more or less in a state of confusion. They are very difficult to separate, owing to the many varieties and intermediate forms. The writer was privileged to work for about three months at the Berlin Herbarium on the HILLEBRAND collection, shortly before the outbreak of the present war, and also at the Gray Herbarium, which enabled him to unravel some of the existing confusion. The present paper places a few species of *Pelea* in their proper positions and also clears up the synonymy of *P. auriculaefolia* Gray. Owing to HILLEBRAND'S misidentification of *P. kauaiensis*, HELLER, evidently relying on HILLEBRAND'S description of that species, described the true *P. kauaiensis* Mann as a new species, namely, *P. cruciata*, which must now remain a synonym.

PELEA SAPOTAEFOLIA Mann, Proc. Bost. Soc. Nat. Hist. **10**:312. 1866.—This species is not represented in the Hillebrand Herbarium. A cotype of MANN'S species is in the Gray Herbarium, "no. 559 leg. *Mann*, Kealia, Kauai." The capsule (only very young capsules are attached to the sheet in a separate pocket) is not cuboid, the leaves are long, whorled (in fours), thin papery, yellowish pubescent underneath especially along the midrib and slightly so on the upper surface.

HILLEBRAND'S two varieties β and γ have nothing in common with *P. sapotaefolia* Mann. His var. β is identical with *P. kauaiensis* Mann so far as the leaves are concerned; a single cuboid capsule (detached) is fastened in a paper pocket. In fact, HILLEBRAND'S label has the name first as *P. kauaiensis*, which he crossed out and wrote underneath "*sapotaefolia* fol. oppositis. Mts. of Waimea,

Kauai"; the following legend appears also on the label: "identical with MANN'S sp., only leaves not ternate, *Knudsen* 38."

HELLER'S *P. cruciata* is identical with *P. kauaiensis* Mann. HELLER'S no. 2870, labeled *P. sapotaefolia* var. β Hbd., has nothing to do with the plant of that name. It cannot be determined, however, as the specimen is in neither flower nor fruit.

Of HILLEBRAND'S var. (?) γ *procumbens*[1] there are two sheets in the Berlin Herbarium, "leg. *Knudsen* no. 165, high mountains of Waimea." This is not a variety of *P. sapotaefolia*, but a distinct species. The writer, in his book on the *Indigenous trees of the Hawaiian Islands*, expressed a similar view, but could make no definite statement, as he had not seen the Hillebrand nor the Harvard collection. HILLEBRAND'S label on the plant collected by *Knudsen* (no. 165) bears the following legend:

> This is probably *P. sapotaefolia;* the leaves agree entirely with *Mann's* no. 557, which is *P. sapotaefolia* fol. opposit., not *P. oblongifolia* as wrongly labeled. It is true that in the specimen there is only one flower in each axil, but on close examination the pedicel is found to rest on a very short peduncle; and in no. 559, the true type of *P. sapotaef.* fol. *3-natis*, there can be distinctly seen, alongside the one developed flower, quite a numerous cluster of small undeveloped buds, so that the inflorescence seems to be considered sub-umbellately many-flowered.

Portion of HILLEBRAND'S specimen leg. *Kn.* no. 165 is in College of Hawaii Herbarium. Of the typical *P. sapotaefolia* H. Mann, the College of Hawaii Herbarium possesses a specimen collected by *Faurie* (*F.* 188), C. H. Herb. no. 12710.

Pelea Gayana, n. sp.—*P. sapotaefolia* Mann var. (?) γ *procumbens* Hbd. Fl. Haw. Isl. 63. 1888.—A small procumbent shrub with terete glabrous branches; leaves opposite, elliptical-oblong, equally acute at both ends, thin chartaceous, glabrous on both sides, 10–13 cm. long, 3.5–4.5 cm. wide, on furrowed petioles 15–20 mm. long, dark green above, pale underneath, the midrib prominent underneath, the lateral veins united by an irregular arched intramarginal nerve; inflorescence in the axils of the leaves, very shortly pedunculate (about 1.5 mm.); pedicels bracteolate in lower and upper third, bracteoles 0.5 mm., pedicels filiform, 8 mm.

[1] Flora Hawaiian Islands, 63. 1888.

FIG. 1.—*Pelea Gayana* Rock; type no. 1972

when in flower, 25 mm. with fruit; flowers very small, sepals broadly ovate, acute, about 1 mm., puberulous; petals ovate, acute, 2.5 mm.; stamens about one-third the length of the petals, all of equal size; ovary deeply lobed, puberulous; capsule puberulous, thin papery, only one locule usually maturing, often with one or two abortive ones, locules divided almost to the base but still united; seeds not seen.

KAUAI.—Swampy forest on the high plateau of Waimea, elevation 4500 ft., collected in company with Mr. FRANCIS GAY of Kauai, who knew the plant by its native name "Kaleiohiiaka"; fruiting March 3, 1909, *Rock*, type no. 1972 in College of Hawaii Herbarium; flowering September 1909, same locality, *Rock* no. 5285 in College of Hawaii Herbarium.

HILLEBRAND'S specimen in the Berlin Museum, *Knudsen* no. 165, belongs here; a portion of this specimen is deposited also in the College of Hawaii Herbarium.

PELEA CINEREA (Gray) Hbd. var. **rubra,** n. var.—*P. oblongifolia* Gray β var. (?) Hbd. Fl. Haw. Isl. 65. 1888; *P. cinerea* (Gray) Hbd. var. δ Rock, not Hbd. in Indig. Trees Haw. Isl. 239. 1913.—Shrub with rambling branches; leaves elliptical to elliptical-oblong, thick chartaceous, glabrous on both sides, dull green, acute at apex, mucronate, rounded at base or subcordate, 7.5–9 cm. long, 3–4.5 cm. wide, on petioles 1.5 cm. long; peduncle 3 mm., stout and quadrangular; the single hirsute pedicel 2 mm.; flowers unknown; capsule hirsute with reddish hair, the cocci (separated) divided to the base, cohering only at the very base, 1.5 cm. long, nearly 1 cm. high, strongly nerved, endocarp hirsute, pale yellowish, and free.

HAWAII.—Lava beds of Huehue, North Kona, fruiting June 6, 1909. *Rock* no. 3565 type in College of Hawaii Herbarium.

This variety of *P. cinerea* was doubtfully referred to *P. oblongifolia* by HILLEBRAND, who collected it in South Kona, Hawaii. Of his fruiting specimen in the Berlin Herbarium only one coccus of each of the two capsules is developed, the others are abortive. This might have misled him, as it cannot be determined clearly whether the cocci are cohering or not. In the writer's specimen, which is identical with that of HILLEBRAND, the carpels are discrete and therefore must be referred to *P. cinerea* (Gray) Hbd. The writer had previously referred it to HILLEBRAND'S var. δ of that species. It is apparently intermediate between *P. cinerea* and *P. elliptica.*

PELEA CINEREA (Gray) Hbd. var. SULFUREA Rock.—This is HILLEBRAND'S β, of which there is only one sheet in the Berlin Herbarium collected on Lanai. No specimen is represented from Maui. The writer collected this variety on the Island of Maui above Makawao slopes of Mount Haleakala. The leaves are pale and more or less glabrous on both sides. The capsule is smaller and sulphur-yellow. HILLEBRAND'S Lanai specimen has darker leaves, with a dirty olivaceous tomentum. A portion of his specimen is in the College of Hawaii Herbarium, also *Rock* no. 8550, from Maui.

PELEA CINEREA (Gray) Hbd. var. HAWAIIENSIS (Wawra) Rock.—*P. hawaiiensis* Wawra, Flora 110. 1973; *P. cinerea* (Gray) Hbd. var. γ Hbd. Flora Haw. Isl. 69. 1888.—Of HILLEBRAND'S specimens (three sheets in Mus. Bot. Berlin) two were collected by him in 1862 at Kawaihaeiuka on Hawaii, the third is from the Kohala chain, Hawaii. A specimen from Kawaihaeiuka ex. herb. Hillebrand is in the College of Hawaii Herbarium, with specimens collected by the writer in South Kona, Hawaii, on Puuwaawaa Hill, June 15, 1909, *Rock* no. 3654.

The writer's no. 10210 belongs here, although the leaves are glabrate or only slightly pubescent, but are of thick leathery texture as in var. *sulfurea*. They were collected in the Kipuka Puaulu near Kilauea on the slopes of Mauna Loa, alt. 4000 ft. July 1911.

PELEA WAWRAEANA Rock, Indig. Trees Haw. Isl. 231. 1913.—This species, while distinct, is closely related to *P. sandwicensis* Gray. In the Gray Herbarium there is a specimen ex. herb. Hillebrand labeled *P. sandwicensis* Gray *microcarpa*, which is identical with *P. Wawraeana*. It was evidently included by HILLEBRAND in *P. sandwicensis*, as he makes no mention of it in his *Flora;* the locality is given as the western end of Oahu. It is the writer's no. 3020 in the College of Hawaii Herbarium.

In the HILLEBRAND collection his var. β of *P. sandwicensis* is marked as var. *macrocarpa* Hbd., and his var: γ of the same species var. *tenuifolia* Hbd.

In the typical *P. sandwicensis* the capsule has the carpels parted half way and in some specimens even more, while *P. Wawraeana* has distinctly cuboid capsules, which are much smaller than in *P. sandwicensis*.

HILLEBRAND'S var. γ *tenuifolia* of *P. sandwicensis* has also a cuboid capsule, but leaves are three in whorl. He says: "otherwise the same as β." This is not so, for *P. sandwicensis macrocarpa* has larger capsules and the carpels are divided to the middle.

PELEA KNUDSENII Hbd. Fl. Haw. Isl. 70. 1888.—In the Berlin Herbarium is only one sheet of this species, but labeled in Hillebrand's handwriting "*Pelea villosa* Hbd. Waimea, Kauai, *Knudsen* no. 210." It is identical with, and answers the description of, *P. Knudsenii*, which is *Knudsen* no. 210. The writer's *P. multiflora* is probably identical with it, but owing to the much larger inflorescence and numerous flowers, often more than 200 on a single inflorescence, it may be reduced to varietal rank as *P. Knudsenii* var. *multiflora* Rock.

The species occurs on the Island of Kauai, while the variety grows on the southern slopes of Mount Haleakala on the Island of Maui.

PLATYDESMA.—In the Gray Herbarium is a leaf mounted and labeled *Melicope grandiflora* U.S. Expl. Exped. Sandw. Isl. The leaf is recognizable at a glance as belonging to the genus *Platydesma;* it belongs unquestionably to *P. campanulatum* Mann. *P. cornutum* Hbd. occurs only on Oahu, while the former species is found on Kauai, Maui, Hawaii, and Oahu. The specific name given by GRAY is *grandiflora* in the manuscript and *grandifolia* in the publication.[2] Another sheet in the Gray Herbarium contains a paper pocket with a fruit and fragments of fruit identical with HILLEBRAND'S *P. cornutum*. The fragments and fruit were communicated to GRAY by Dr. WM. T. BRIGHAM, of Honolulu, with the remark "Sandwich Islands, sem. in loculis 6" (evidently referring to the number of seeds in each locule). It bears the name of *Melicope* (?) *grandiflora* Gray in GRAY'S handwriting. He evidently associated the fruit collected by BRIGHAM with the leaf shoot collected by the United States Exploring Expedition. A careful illustration of a flower and fruit of what is HILLEBRAND'S *P. cornutum* accompanies the specimen.

PELEA AURICULAEFOLIA A. Gray, Bot. U.S. Expl. Exped. 343. *pl. 36.* 1854.—No specimen exists of this species in the Gray Her-

[2] U.S. Expl. Exped. 14: 354. 1854.

barium. HILLEBRAND'S single specimen in the Berlin Herbarium marked *Platydesma auriculaefolia* (Gray) Hbd. is certainly not a *Pelea* but a *Platydesma*. The leaves in the specimen are opposite and not ternate, and are somewhat auriculate. It is neither in flower nor in fruit. This plant of HILLEBRAND'S is identical with the writer's var. *sessilifolium* of *Platydesma campanulatum* collected in the Kohala Mountains on Hawaii, from whence HILLEBRAND'S specimen originates. *Platydesma auriculaefolia* Hbd. is not a synonym of *Pelea auriculaefolia* Gray, but a synonym of *Platydesma campanulatum sessilifolium* Rock. The plant represented on the excellent plate in the atlas of the United States Exploring Expedition is a typical *Pelea*.

PELEA GAYANA and P. CINEREA var. RUBRA.

Pelea recurvata, n. sp.—*P. kauaiensis* Hbd. (not H. Mann), Fl. Haw. Isl. 64. 1888.—A small tree 5 m. high with rambling branches (teste HILLEBRAND); leaves opposite, ovate or elliptico-oblong, 10–12.5 cm. long, 5–6.5 cm. wide, on petioles 1.75–2.5 cm. long, moderately acuminate, chartaceous, marginal nerve remote from the edge, with one or two sets of meshes between, shining above, clothed underneath, especially along the midrib, with a dense velvety or cobwebby villosity; flowers small, one or more in a cluster, on filiform pedicels 4–6 mm. long, which are bracteolate at the base; sepals ovate, 2–3 mm. long; petals thin, 3–5 mm. long; capsule thin, deeply 4-parted to near the base, the narrow elongate cocci divaricate and strongly recurved, about 12 mm. long, 4 mm. broad, keeled at the upper suture, one or more often abortive.

KAUAI.—Waimea at elevations of 2000–3000 ft.; *Knudsen* no. 64 in Herb. Hillebrand Berlin Bot. Museum is the type, and part of the type is in College of Hawaii Herbarium no. 12711.

COLLEGE OF HAWAII
HONOLULU

SECRETORY CANALS OF RHUS DIVERSILOBA

JAMES B. MCNAIR

In *Rhus diversiloba* T. and G. the resin passages are situated in the roots, stems, leaves, and fruit in the phloem of the primary vascular bundles. In addition, there are others in the secondary bast of the stem and root.

The root contains a single wide resin canal in each of the phloem portions of the primary bast. In the secondary bast, resin canals in concentric circles with smaller lumina are successively added. After the secondary phloem is formed in the root, the xylem and phloem are formed exactly as in the stem.

In the stem the phloem portion of the primary bundles is separated from the parenchymatous outer cortex by a strong bundle of sclerenchymatous (bast) fibers of crescent-shaped transverse section. These fibrous bundles are almost in contact with one another at their margins, and thus constitute a ring around the outer cortex. Outside of this sclerenchymatic ring no resin passages are found, but large ones are located immediately within it, one in the phloem of each vascular bundle. In the secondary cortex, which is formed later internally, new canals are formed successively in the strands of the bast. The cortical passages of the secondary bast are connected in the internodes by more or less numerous tangential anastomoses, and thus combine to form a more or less complete cylindrical network in the bark concentric with the stem cylinder. The cortical passages in the nodes anastomose with one another. The leaf passages extend up the internode to the plexus of anastomoses.

The vascular bundles which pass into the petiole are arranged in curves to follow the outline of the petiole in its transverse section. These branch when they reach the leaflets. The resin passages are arranged in the petiole as in the primary vascular bundles. The canals may be absent in the weaker bundles, however.

In the midrib of the leaflets the fibrovascular system is divided into two parts. One, the superior, the ventral, is formed of 3

reunited bundles placed under the endophloem; the other, the dorsal, has 5–7 bundles arranged in an arc, and has also 5–7 resin passages in the phloem parts.

All lateral ribs contain at least one passage on their dorsal sides, which is in the phloem as usual. Some of the resin canals seem to end blindly in the spongy parenchyma and palisade parenchyma, while others apparently anastomose in a reticulate manner like the vascular bundles which they accompany.

TRECUL (**7**) noticed in *Rhus Toxicodendron* L., to which *R. diversiloba* is very closely allied, the obstruction of the resin canals at the base of the petiole just before the fall of the leaves. This obstruction is effected by an increase in the parietal cells of the canals, and thus constitutes an instance of tylosis, similar perhaps to the obliteration of the old canals in the bark. The enlarged cells divide and the new ones produce more of the same kind. Soon the ducts are seen on the outside of the parenchyma at the place of insertion of the leaves. At a small distance away in the leaflet the passages have a normal appearance and are filled with sap.

Resin passages in *R. diversiloba* are found also in the mesocarp of the fruit and in the hypocotyl and cotyledons of the embryo, likewise in the phloem. It is interesting to notice how early in the life of the plant these organs of secretion are found, and yet they are confined from first to last in the phloem group.

According to SIECK (**5**), the resin canals of the Anacardiaceae are of schizolysigenous origin.[1] The first development of the intercellular cavities can readily be observed in *R. diversiloba*, which has good clear channels. In the beginning the evolution of the resin tube in this plant is clearly schizogenous. It forms itself from a little group of cells individually much narrower than the other parenchyma cells. A short slit soon appears toward the center of the group. When this slit enlarges itself, a little of the resinous sap appears. The opening, first irregular in outline, enlarges to a channel of considerable size with a regular circular outline and is bordered by narrow cells. This is by far the form most commonly

[1] It should be stated that SIECK worked with *Anacardium occidentale*, which is not very closely related to *Rhus diversiloba*, a fact which may explain the apparent difference in origin of the secretory canals.

noticed and is plainly schizogenous. Some of the secreting cells may eventually break down altogether, to leave their secretions in the cavity formed by their disintegration and thus be designated lysigenous in character. Cavities so appearing in my investigations of this plant may have been due to imperfect sections. At any rate, lysigenous cavities are apparently in the minority.

If these observations be compared with previous works on other Anacardiaceae, it will be seen that there are no essential differences in the arrangement of the intercellular secretory reservoirs. Which genera should be poisonous, or why their poisons should vary, either in physiological action or in chemical composition, cannot be deduced from this part of their anatomies.

Plants other than the Anacardiaceae that secrete resin, emulsions of gum-resin, etc., in passages are as follows: Coniferae, Alismaceae, Aroideae, the tubifloral Compositae, Umbelliferae, Araliaceae, Pittosporeae, many species of *Mamillaria*, Clusiaceae, and *Ailantus* and Bruceae of the Simarubeae.

The abundance and comparatively large size of the resin ducts, together with their fusing, make an intercommunicating system. When a wound is made, the sap and its poison are quickly pressed out, either by the tension of the elastic walls of its own cells or by a combination of both. In the spring the sap is very watery, while the autumn product is much thicker, granulous, and slower in exudation. The sap, which is properly an emulsion, is, when first expressed, white or light gray in color, and as it quickly coagulates and browns in the air, it forms an efficient covering for the wound. The sap is darkened in the air mainly by oxidation, as has been shown in a former paper (3): first, when deprived of oxygen the sap darkens but very slowly; secondly, when in the presence of oxygen the sap darkens rapidly; and finally, ultimate chemical analyses of the sap before and after darkening show an appreciable difference only in the oxygen content.

Under the microscope the freshly exuded sap is in part a colorless liquid and in part made up of minute globules. Very soon some of these globules become dark brown, while the fewer remaining globules continue to be colorless. While this change has been taking place, oblong rectangular colorless crystals separate out. The first crystals to separate are larger than those which form

later. This process of crystallization probably has its cause in the evaporation of the menstrum. If these crystals be viewed through a petrographic microscope, they are seen to be birefringent, similar perhaps to those noticed by WIESNER (8) in the sap of *R. vernicifera*. On adding water the light colored globules disappear, but the brown ones remain. The addition of alcohol, on the other hand, causes the solution of the brown globules.

The freshly exuded resinous sap of *R. diversiloba* has been shown to be the only part of the plant capable of producing dermatitis (2). Consequently those portions of the plant that do not contain the resin ducts do not have this kind of toxic effect. The non-toxic portions are the anthers, pollen, xylem, trichomes, epidermis, and cork cells. The poison has also been shown to be non-volatile, although it may be carried by the particles of soot in smoke.

INUI (1) has noticed that the amount of secretion of *R. vernicifera* is influenced by the conditions of light and atmospheric humidity. In potted plants the secretion lessened when carbon assimilation was hindered. Similarly secretion was greater in damp than in dry air. This secretion therefore seems to bear a relation to transpiration and hence to turgor. As the degree of turgor varies indirectly with the amount of transpiration, other things being equal, secretion would be least when transpiration is greatest. Turgor, too, is a necessary accompaniment of growth; flaccid tissues do not grow larger. If those influences which affect *R. vernicifera* have a similar action on *R. diversiloba*, then secretion, and consequently the plant conditions for poisoning, would be greatest during that time of the year when the growth of the plant is most active and the tissues least resistant, in the spring. Obviously enough, when the plant is in full leaf and when growth has diminished, its resistance to injury will be greater and its liability of poisoning less.

In autumn the charming appearance of the luxuriant foliage, when it turns to many shades of scarlet and bronze, speaks a flagrant warning to its victims and is only especially alluring to the unsuspecting. Nevertheless, either the amount or the virulence of the poison in the autumn leaves is less than that of the normal mature leaves (3). Of the autumnal leaves the red are less toxic than the yellow, and when the leaves have finally withered and

fallen they are non-toxic. During that period of the year when the plant is leafless the risk of its producing poisoning is least.

This theoretical consideration of the liability of *Rhus* poisoning from a botanical point of view has its counterpart in clinical statistics. The latter lend analogous evidence to the conclusion that spring has the greatest number of cases (see frequency polygons) (**9**).

The number of cases of dermatitis from *R. diversiloba* is influenced, not only by the condition of the plant, but also by those conditions which tend to make individuals come in contact with it or with substances coated with its poisonous sap. ROBERT LOUIS STEVENSON (**6**) describes a tramp in California woods as follows:

> We struggled toughly upward, canted to and fro by the roughness of the trail, and continually switched across the face by sprays of leaf or blossom. The last is no inconvenience at home; but here in California it is a matter of some moment. For in all woods and by every wayside there prospers an abominable shrub or weed, called poison-oak (*Rhus diversiloba*).

Many low plants seek the shelter of the *Rhus diversiloba* shrubs, and some of our loveliest flowers, such as Clarkias, Godetias, Collinsias, Brodiaeas, and Larkspurs, seem to realize that immunity from human marauders is to be had within its safe retreat. JOHN MUIR (**4**) "oftentimes found a curious twining lily (*Stropholirion californicum*) climbing its branches, showing no fear but rather congenial companionship." The desire to gather spring wild flowers is often greater than the fear of *Rhus diversiloba*. Circumstances thus combine to bring victim and culprit together at the time when the culprit is capable of doing the most harm. It may truthfully be said in regard to this poisonous plant, as is said of the Scotch thistle, "no man provokes it without fear of punishment."

Summary

1. The intercellular secretory canals of *Rhus diversiloba* T. and G. are found in the roots, stem, leaves, and fruit in the phloem of the primary vascular bundles. There are other secretory canals situated in the secondary bast of the stem. They are found also in the phloem of the mesocarp of the fruit and in the hypocotyl and cotyledons of the embryo.

2. Their formation may possibly be schizolysigenous. In the beginning they are clearly schizogenous.

3. There are no essential differences in the arrangement of the intercellular secretory reservoirs between the poisonous and non-poisonous Anacardiaceae.

4. From an anatomical standpoint there is no reason why the poisons of the Anacardiaceae should vary either in physiological action or in chemical composition.

5. The fresh sap emulsion is the only part of the plant capable of producing dermatitis.

6. Those portions of the plant that do not contain the resin ducts do not normally have this kind of toxic effect.

7. The non-toxic portions are the anthers, pollen, xylem, epidermis, cork cells, and trichomes.

8. The liability of poisoning from *R. diversiloba* tissues decreases as follows: immature leaves and flower parts (except anthers and pollen), mature leaves, green stems, young roots, woody stems, and woody roots.

9. The liability of poisoning from *R. diversiloba* is greatest in the spring, less in the summer and fall, and least when the plant is leafless.

PASADENA, CAL.

LITERATURE CITED

1. INUI, T., Gummiharzang d. Lackbaumes, U.S.W. Bot. Centralbl. **3**:352–. 1900.
2. MCNAIR, JAMES B., The transmission of *Rhus* poison from plant to person (*Rhus diversiloba* T. and G.). Jour. Infect. Diseases **19**:429–432. 1916.
3. ———, The oxidase of *Rhus diversiloba*. Jour. Infect. Diseases **20**:485–498. 1917.
4. MUIR, JOHN, My first summer in the Sierra. Boston and New York. 1911 (pp. 34, 35).
5. SIECK, W., Die schizolysigenen Secretbehälter. Jahrb. Wiss. Bot. **27**:227. *pls. 6–9*. 1895.
6. STEVENSON, R. L., Napa wine III. In the valley. The Silverado squatters. 1883.
7. TRECUL, M. A., Des Vaisseaux propres dans les terebinthinees. Compt. Rend. **65**:17. 1867.
8. WIESNER, JULIUS, Die Rohstoffe des Pflanzenreiches **1**:299. 1900.
9. MCNAIR, JAMES B., Pathology dermatitis venenata from *Rhus diversiloba*. Jour. Infect. Diseases **19**:419–428. 1916.

CURRENT LITERATURE

BOOK REVIEWS

The organism as a whole

The author of this book[1] in his previous writings has concerned himself with particular processes and activities of the organism, but has never given us any adequate consideration of that remarkable order and harmony which make the organism a whole and not merely an aggregate of parts. The title of the book arouses the hope and justifies the expectation that we shall find in it something in the way of a synthesis or some attempt at least to formulate the problem of organic order and harmony in physico-chemical terms. To what extent the book accomplishes this will appear more clearly as we consider its contents.

In the preface the author says, "in this book an attempt is made to show that the unity of the organism is due to the fact that the egg (or rather its cytoplasm) is the future embryo, upon which the Mendelian factors in the chromosomes can impress only individual characteristics, probably by giving rise to special hormones and enzymes." Apparently this conception of the egg cytoplasm and chromosomes is the chief thesis of the book, for it is stated repeatedly in almost the same words. By way of proof, some well known cases of visible cytoplasmic differentiation in animal eggs are cited and their apparent relation to the future embryo is pointed out, but as regards the action of the Mendelian factors the reviewer has not been able to find anything except surmises, suggestions, and opinions, and these do not carry us beyond the original statement. Moreover, no attempt is made to show how the unity of the organism results from this situation in the egg or how the situation itself arises. As LOEB states it, the case looks amazingly like one of pre-established harmony. The cytoplasmic differentiations are there and the Mendelian factors are there, apparently without any previous relation to each other, and it does not appear how they have come to be there. It is difficult to discover where the unity lies.

The second thesis of the book seems to be that the existence of purposeful and harmonious organisms is explicable in mechanistic terms on the basis of evolutionary theory, provided we substitute the De Vriesian for the Darwinian conception. In support of this thesis the stock arguments are presented: (1) that mutations are inherited, while fluctuating variations are not; and

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[1] LOEB, JACQUES, The organism as a whole from a physico-chemical viewpoint. pp. viii+379. New York: Putnam Sons. 1916.

(2) that organisms which are not purposeful and harmonious cannot persist. We look in vain for any consideration of the organism as a whole, that is, of the nature of its wholeness. There is no discussion of the morphological problem, but structure is simply accepted or assumed as required, and the author is chiefly concerned with certain chemical aspects of life.

If, however, the book is not exactly what its title leads us to expect, it nevertheless contains a great variety of facts, suggestions, and hypotheses concerning many aspects of biology, and these are all presented in the author's usual interesting and persuasive style. It is quite impossible even to mention all the various fields which the author enters, but a brief survey of chapters will indicate the range of the book.

In an introductory chapter CLAUDE BERNARD'S "design," DRIESCH'S "entelechy," and VON UEXKÜLL'S "supergenes" are briefly considered and discarded as superfluous.

The contents of the second chapter are indicated by its title: "The specific difference between living and dead matter and the question of the origin of life." LOEB refutes very effectively the argument for a fundamental similarity between organisms and crystals. The organism differs from the crystal and other inorganic systems in that it synthesizes its own specific substance out of non-specific materials. He then argues for the immortality of the body cell, but without discussion of the phenomena of senescence, and finally reaches the conclusion that life is either eternal or that there must be synthetic enzymes which form molecules of themselves from a nutritive solution. Apparently he fails to see that such enzymes offer no solution of the problem of the origin of life, for, according to his own definition of living things, these enzymes must themselves be alive.

The third chapter, "The chemical basis of genus and species," discusses specificity in grafting, blood and serum specificity, etc., and concludes that the basis of specificity is in the proteins. The next two chapters, "Specificity in fertilization" and "Artificial parthenogenesis," are in large measure an account of the work of LOEB and his students, and contain little of importance that has not already appeared in the author's earlier books. Recent work on the problem by F. R. and R. S. LILLIE and others is briefly mentioned, but the author's conclusions remain essentially unaltered.

The sixth chapter, "Determinism in the formation of an organism from an egg," is an argument in support of the view that the egg cytoplasm is the embryo in the rough. The cases of visible cytoplasmic differentiation in animal eggs and its apparent relation to later development are cited, but no mention is made of the centrifuge experiments which demonstrated that, in most cases at least, this visible differentiation is not an essential feature in further development. After some consideration of the development of isolated blastomeres, LOEB concludes that the only regulation in the egg consists in a flow of materials, but he neglects to account for the remarkably orderly character of the flow.

Following is a chapter on "Regeneration," which begins with a statement of SACH'S theory of formative substances. The reviewer finds much to criticize in this chapter, since his own work in this field has led him to very different conclusions from those reached by LOEB, but only a few points of more general interest need be noted here. Special substances are postulated to account for all phenomena of regeneration, there is no adequate discussion of nor even reference to other hypotheses, and most of the experiments cited are those of LOEB and his students. In the discussion of regeneration in plants only the author's experiments on *Bryophyllum* are mentioned. One would never even suspect from reading the book that the problem of regeneration or experimental reproduction had ever received any attention from the botanists. MCCALLUM'S work is completely ignored. In the case of *Bryophyllum*, which is discussed at some length, LOEB'S argument is briefly this: certain substances determine the growth of a particular organ, for example, a growing tip, and the growing organ attracts these substances. In other words, the substances are necessary to make the organ grow, while on the other hand, it must begin to grow in order to obtain these substances. These substances are assumed to be in the fluids of the body and to be carried by these except in so far as they are "attracted" by particular growing tips. If this is the case, how is it possible that one growing tip can prevent another, perhaps in its immediate vicinity, from obtaining *any* of the substance necessary for its growth? But this is what LOEB assumes and asks us to believe.

In discussing certain experiments on *Planaria*, BARDEEN'S earlier conclusions are accepted and no mention is made of the fact that BARDEEN himself showed in later work that they were incorrect, and that more recent work has still further demonstrated that the factors concerned are very different from those which LOEB postulates. The author's experiments, made some 25 years ago, on the effect of gravity in determining the polarity of the hydroid *Antennularia* are described, but there is no discussion or even mention of the fact that other investigators have been quite unable to confirm them.

The flow of substances, assumed by LOEB to occur in pieces of the stem of the hydroid *Tubularia* toward one pole or the other as the facts of regeneration demand, is entirely without any basis of evidence, and the simultaneous regeneration of hydranths or partial hydranths at both ends of a short piece with no stem between them presents difficulties to this interpretation. Since the short piece produces hydranths and these hydranths occupy its whole length, it must have contained enough of the formative substances to produce them. If this is the case, why is any flow from other parts necessary for the production of a hydranth in longer pieces, as the hydranth-forming region must have enough of it to develop a hydranth? Moreover, if a short piece of the stem can transform itself completely into one or more hydranths or partial hydranths without the presence of other parts, how can the development of the hydranth be determined by the influence of other parts, as LOEB maintains? Further criticisms of this chapter might be made, but perhaps

these are sufficient to show that LOEB's interpretations throw no light on the problem.

Chapter VIII, "Determination of sex, secondary sexual characters, and sexual instincts," deals first with the cytological basis of sex-determination. LOEB accepts in their most extreme form the conclusions of the cytologists concerning the "sex-chromosomes," and says that "thus far all the facts agree with the dominating influence of certain chromosomes upon sex-determination." Actually, however, these facts, assuming that they are all facts, have been interpreted very differently by different authors. Sex-determination in plants is mentioned in only two brief sentences. The discussion of the physiological basis of sex-determination is largely concerned with sex-hormones, experimental and parasitic castration, and the influence of nutrition on sex. The intersexual forms of the moth *Lymantria* obtained by GOLDSCHMIDT are described, but without comment.

The account of "Mendelian heredity and its mechanism" in chapter IX begins with a brief outline of Mendelian theory and of MORGAN's hypothesis of localization of the Mendelian factors in the chromosome, concluding with the statement "biology has thus reached in the chromosome theory of Mendelian heredity an atomistic conception, according to which independent material determiners for hereditary characters exist in a linear arrangement in the chromosome." The author then inquires "what makes a harmonious organism out of this kaleidoscopic assortment?" The answer is that the egg cytoplasm is the embryo in the rough, and that each determiner in the chromosomes gives rise to one or more substances which influence various parts of the body. But when we ask how the egg cytoplasm comes to be the embryo, and in the rough, and how it happens that the substances produced are adjusted to the different regions of the cytoplasm, we find no answer except the assertion that evolution can produce harmonious organisms, because those that are not harmonious are eliminated.

Chapter X on "Animal instincts and tropisms" adds nothing essential to LOEB's previous discussion of the subject, and is open to the same criticisms. The chapter is devoted largely to the consideration of reactions to light and the attempt to show that they are in accord with the Bunsen-Roscoe law of photochemical reactions, according to which the chemical effect is within certain limits equal to the product of intensity into duration of illumination. There is but little discussion of fact or theory which does not agree with LOEB's conclusions. As regards the trial and error theory, LOEB says that it has been refuted by practically all workers in the field. Students of animal behavior will be interested to discover that the question has been settled.

"The influence of environment," chapter XI, is devoted largely to consideration of the influence of temperature, the temperature coefficient of physiological processes, salt antagonisms, and balanced solutions. This is followed by a chapter on "Adaptation to environment," which is somewhat less extreme than some of the author's earlier discussions of the subject, but

in which his skepticism as to the occurrence of adaptation is clearly evident. LOEB seems to believe that if a case of apparent adaptation can be stated in terms of the action of particular substances on particular parts or stages, it is thereby removed from the category of adaptation. Actually of course this line of reasoning does not touch the real problem, for the harmonious relations between substance and organ of apparent specificity, time, or intensity of action, may themselves be adaptations. A chapter on "Evolution," consisting of three pages, is little more than an acceptance of the De Vriesian as opposed to the Darwinian conception of the mechanism of evolution.

The final chapter, "Death and dissolution of the organism," begins with an interesting consideration of autolysis and its relation to the cessation of oxidations, lack of oxygen, and change in hydrogen ion concentration. Death in the higher animals, he says, is due to cessation of oxidations. The statement "it is an unquestionable fact that each form has a quite definite duration of life" is not in agreement with recent experimental work on some of the lower animals, and to say that "no species can exist unless the natural life of its individuals outlasts the period of sexual maturity" is to ignore the fact that various forms, not only among the protozoa which LOEB regards as immortal, exist for many generations, probably indefinitely, with only agamic reproduction. Are such forms also immortal? As regards the protozoa, however, he fails to note that the "immortality" depends upon reproduction. Any protoplasm concerned in reproduction is just as immortal as protozoan protoplasm. This sort of immortality depends upon the processes of rejuvenescence associated with reproduction, and is merely the continuity of life through the reproductive process. As might be expected from the suggestion in chapter II that the body cell is immortal, LOEB agrees with METCHNIKOFF in regarding senescence and death as essentially an accident due to the formation in the body of poisons through bacterial action or otherwise. Special chemical substances are the cause of death as well as of most of the phenomena of life.

This then is apparently LOEB's conception of the organism as a whole, a "kaleidoscopic assortment" of material factors or determiners located in the chromosomes, producing substances which act on another assortment of materials in the cytoplasm. In chapter II he says "biology will be scientific only to the extent that it succeeds in reducing life phenomena to quantitative laws." Nevertheless, his interpretations are predominantly qualitative, and in various cases he has ignored quantitative interpretations offered by others. We find, for example, no mention even by way of refutation of RIDDLE'S quantitative hypothesis of sex. The evidence in favor of a quantitative conception of polarity and of initiation of differentiation is not considered, and no mention is made of the quantitative hypotheses of senescence, which, by the way, can be interpreted in terms which are completely in accord with the autocatalytic theory of growth in favor of which LOEB has repeatedly declared

himself. There seems to be a certain inconsistency in this preference for qualitative interpretations. If scientific biology is essentially quantitative, as LOEB maintains, we have the right to demand adequate grounds for his rejection or failure to discuss quantitative as opposed to qualitative interpretations.

Few biologists of the present day will deny the importance of chemical or transportative correlation, that is, the production, transportation, and action in the organism of chemical substances, many of which are supposed to be specific. There is, however, another sort of physiological correlation, namely, transmissive or conductive correlation, which finds its highest development in the nervous system. In this sort of correlation the essential feature is the transmission of energy rather than the transportation of materials. There can be no doubt that in organisms which possess a differentiated nervous system this is the chief factor in maintaining the integration of the organism as a harmonious whole. But biologists are very generally agreed that the nervous system adds nothing new to the organism, for transmissive correlation exists even where there is no visibly differentiated nervous system. In fact, the nervous system is the structural and functional expression of transmissive relations between parts which exist both embryologically and phylogenetically before its development. Unless we assume the existence of an entelechy or supergenes or some other non-mechanistic ordering and controlling principle, we cannot escape the conclusion that the starting-point of physiological integration is to be found in the initiation and transmission from one part to another of dynamic changes, not of material substances.

In a discussion of the organism as a whole we should expect to find something concerning the nervous system, and how it has become of such importance in physiological integration. LOEB, however, merely refers in the preface to his "comparative physiology of the brain" as supplementing the present book. The German edition of that work appeared in 1899. It seems to many of us that after 18 years there might at least be something to add to the original discussion, particularly as regards the integrating function of the nervous system or of protoplasmic conduction in general. Apparently, however, transmission, conduction, and nervous function possess no fundamental significance for the author in relation to the wholeness of the organism.

The analogy between the biological individual, the organism, and the social organism, the state, has often been noted both by biologists and sociologists. The reviewer believes that there is more than an analogy here. Both the organism and human society represent the reactions of living protoplasm to its environment, and in the integration of human individuals into an orderly and harmonious whole we find a fundamental similarity to the process of physiological integration within the organism. A moment's thought is sufficient to show that in the integration of human beings into an orderly community or state the transmissive relations are the primary factors. The

production and interchange of substances among human beings, which we know as barter and exchange or commerce, can never of itself integrate those concerned into an orderly and harmonious whole, a tribe or nation. Government of some sort, that is, authority and its transmission, is the real integrating factor, and commercial relations do not assume an orderly harmonious character until at least some degree of integration has taken place.

LOEB is attempting to conceive the organism as a whole in terms of the commercial relations between its parts. This is as if one should attempt to interpret a nation or state and its origin in terms of the production and exchange of commodities between its constituent members or groups. The one attempt is as futile as the other. Actually LOEB has failed to see the organism as a whole because he has been so engrossed with the particular activities of its various parts and their relation to environment. Evidence is rapidly accumulating to show that control, that is, government in the organism, is a physiological fact, and the primary fact in the integration of the individual, that such control originates in quantitative differences in the velocity of metabolic reactions and the associated protoplasmic differences together with the transmission of energy changes resulting from these differences rather than in the transportation of substances, and that the nervous system is morphologically and physiologically merely the expression of the transmissive relations which exist from the beginning of individuation. This conception is not only supported by many lines of evidence, but it comes much nearer LOEB's definition of scientific biology as the reduction of life phenomena to quantitative laws than does his own interpretation in terms of formative or nutritive substances. Certainly the egg is the embryo in the rough, as LOEB maintains, and so is any other reproductive cell or cell mass, but since the embryo and the organism developing from it are orderly and harmonious wholes, the egg and other reproductive bodies must also be wholes of the same sort. It is here that we come face to face with the problem of the organism as a whole, and LOEB offers us nothing but the bare assertion, oft repeated, that the egg is the embryo in the rough, and this is merely the statement of the problem, not the solution. He has contented himself with this mere statement of the real problem and has passed on to devote himself to the innumerable details of the activity of the organism in which the wholeness is already established and effective. If this were all that mechanistic biology has to offer toward the solution of the problem of the organism, the vitalist might rest content.

If we search in vain for the organism as a whole in the book, however, there is nevertheless much of interest. It must be admitted that those familiar with LOEB's earlier books will find little that is new, particularly in certain chapters, and that often there is no consideration of the work of others, but, as a statement of LOEB's conception of the organism, the book cannot fail to interest the biologist, even though, or perhaps because, he will find himself unable to assent to many of its conclusions.—C. M. CHILD.

NOTES FOR STUDENTS

Transpiration studies.—An excellent review of recent investigations on transpiration, by KNIGHT,[2] includes the principal contributions for the five years previous to 1916. Conspicuous among the more recent investigations is that by BRIGGS and SHANTZ[3] upon the comparison of evaporation from various types of atmometers and free water surfaces on shallow and deep tanks, with transpiration from alfalfa (*Medicago sativa*). The departure of the hourly evaporation rate of the porous cup atmometers from the hourly transpiration rate of the alfalfa seems to be due largely (1) to the marked increase in the evaporation over transpiration during the night hours; (2) to the more marked response of the atmometers to changes in wind velocity; and (3) to the lack of proportionate response on the part of the atmometers to changes in solar radiation. The departures amount to 90 per cent for the deep tank, 50 per cent for the white cylindrical atmometer, 40 per cent for the brown cylinder, the white sphere, and the Bellani plate, and 17 per cent for the shallow blackened tank, showing no very close correspondence for any of the systems, but decidedly the best approximation in the last mentioned. In such a tank, 91 cm. in diameter and 2.5 cm. high, the water was automatically maintained at a depth of 1 cm.

In view of the divergence of the evaporation rates from the two tanks employed in these experiments, it becomes evident that THOMAS and FERGUSON[4] have not taken into account all the variables in their effort to obtain a law of evaporation from circular surfaces. This was sought primarily for use in standardizing atmometers and other instruments for comparison of water loss with that from the plant in the process of transpiration. Their conclusion that evaporation from a circular water surface is not proportional to its area was already familiar to us, and has been emphasized not only in the investigation cited but also by Livingston.[5]

To facilitate critical studies of transpiration, BLACKMAN and KNIGHT[6] have devised an apparatus for controlling air movements about plants under investigation and have been able to have constant currents up to a speed of 25 m. per minute. Using this apparatus and otherwise securing carefully

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[2] KNIGHT, R. C., Recent work on transpiration. New Phytol. **16**:127–139. 1917.

[3] BRIGGS, L. J., and SHANTZ, H. L., Comparison of the hourly evaporation rate of atmometers and free water surfaces with the transpiration rate of *Medicago sativa*. Jour. Agric. Research **9**:277–292. 1917.

[4] THOMAS, NESTA, and FERGUSON, ALLAN, On the reduction of transpiration observations. Ann. Botany **31**:241–255. 1917.

[5] LIVINGSTON, B. E., Atmometry and the porous cup atmometer. Plant World **18**:51–74. 1915.

[6] BLACKMAN, V. H., and KNIGHT, R. C., A method of controlling the rate of air movement in transpiration experiments. Ann. Botany **31**:217–220. 1917.

controlled conditions, KNIGHT[7] has performed experiments with various plants with results which show no close agreement between stomatal opening and rate of transpiration, but which tend to demonstrate that the water content of the leaf is an important factor in controlling its water loss by transpiration, and further that stomatal aperture is not reduced by slight water deficiency in the leaf, but is very sensitive to light changes. On the whole, his results support LIVINGSTON's contention of the regulatory importance of "incipient wilting," and are directly opposed to DARWIN's theory that stomatal aperture plays the primary rôle in the regulation of transpiration.

Working with detatched leaves and with potted plants, MARTIN[8] has confirmed previous conclusions in finding that films of Bordeaux mixture cause decided acceleration in the rates of transpiration, and that their influence is apparent as soon as the spray dries upon the leaves. More recently results of the same nature were obtained by SHIVE and MARTIN,[9] using cobalt chloride paper. The indices of the transpiring power of the sprayed leaves are shown to be rather more than 20 per cent higher than for the untreated leaves of the same plant. It is also interesting to note that the investigators express their confidence in the accuracy of the results obtained by the cobalt chloride method, which may now be regarded as a reliable method especially adapted to field use.

Not only are fungicides instrumental in increasing transpiration, but the fungi themselves may also act in a similar manner, as has been shown by WEAVER[10] for cereal rusts. Here the increase in transpiration occurs about the time the pustules break through the epidermis, and the amount of increase is closely related to the pustular area.

Experimenting upon the relations expressed in the comparison of the relative water loss from the plant and the atmometer, termed by LIVINGSTON "relative transpiration," KNIGHT[11] finds that this does eliminate the influence of changes of temperature and relative humidity on rate of transpiration. He asserts, however, that "relative transpiration" does not necessarily represent changes in the intrinsic transpiring power of a plant unless conditions of air movement are constant. This is because of the unequal response of plant and atmometer to changes in wind velocity.—GEO. D. FULLER.

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[7] KNIGHT, R. C., The interrelations of stomatal aperture, leaf water-content, and transpiration rate. Ann. Botany **31**:221–240. 1917.

[8] MARTIN, W. H., Influence of Bordeaux mixture on the rates of transpiration from abscissed leaves and from potted plants. Jour. Agric. Research **7**:529–548. 1916.

[9] SHIVE, J. W., and MARTIN, W. H., The effect of surface films of Bordeaux mixture on the foliar transpiring power in tomato plants. Plant World **20**:67–86. 1917.

[10] WEAVER, J. E., The effect of certain rusts upon the transpiration of their hosts. Minn. Bot. Studies **4**:379–406. 1916.

[11] KNIGHT, R. C., "Relative transpiration" as a measure of the intrinsic transpiring power of the plant. Ann. Botany **31**:351–360. 1917.

Grasslands and forests of Washington.—A recent study by WEAVER[12] of the vegetation of adjacent portions of Washington and Idaho affords an excellent example of modern ecological investigation. After a sketch of the physiography and geology of the region, the results of quantitative studies of the principal physical factors involved are reported. Temperature, rainfall, evaporation, and soil moisture data are given, the last two receiving most emphasis, as they express the important aspects of the water relationship of a vegetation in which the available moisture is undoubtedly the limiting factor. A preliminary report of the evaporation studies was previously made and reviewed in this journal,[13] and the present more complete report only tends to confirm the conclusion that the differences of the rates of evaporation in the various plant communities are sufficient to be important factors in causing succession. The studies of soil moisture also show that this important factor varies in amount directly with the order of the occurrence of the various communities in the order of succession. Incidentally it may be noted that the soil of the *Thuja* association has a very high water holding capacity, showing during the months of July and August a supply of "growth water" of over 40 per cent, thus providing for the development of the very complete mesophytism seen in this climax conifer forest.

The western conifer forests here show a succession from shrub of xerophytic character through *Pinus-Pseudotsuga*, *Larix-Abies* associations to the luxuriant conifer forest composed almost exclusively of *Thuja plicata*. The secondary species of this forest are carefully considered, as well as the reforestation of cutover areas and burns.

The scrub formation dominated by *Artemisia tridentata* and the hydrarch succession from ponds and streams are described, but perhaps aside from the forest the most important and interesting community is the grassland termed "prairie-plains formation" and dominated by *Agropyron spicatum* and *Festuca ovina*. It presents seasonal aspects varying from rich grassy verdure during the comparatively moist spring and early summer, to the sere brown of the arid late summer. The soil moisture determinations show the gradual depletion of growth water from the surface stratum, where it exists in June to the depth of 5 ft., by the middle of August. The response to this distribution of moisture is seen in the luxuriant spring growth and early flowering of the comparatively shallow rooted grasses which dominate the community, and the entire absence of late blooming grasses. It is also apparent in the development of extensive root systems in such conspicuous herbaceous plants as *Balsamorhiza sagittata*, *Hieracium Scouleri*, and *Lupinus ornatus*. This extensive root development has been carefully studied by the same investigator,[14]

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[12] WEAVER, J. E., A study of the root systems of prairie plants of southeastern Washington. Plant World **18**:227–248; 272–292. *figs. 18*. 1915.

[13] BOT. GAZ. **59**:71–72. 1915.

[14] WEAVER, J. E., A study of the vegetation of southeastern Washington and adjacent Idaho. Univ. Neb. Studies **17**:1–114. 1917.

who finds the generalized root type most extensively developed and a penetration of 60–70 inches not uncommon.

The reports abound in interesting details too numerous to mention in a review, are carefully organized and well illustrated with graphs, drawings, and photographs, forming a notable contribution to our knowledge of the vegetation of an unusually interesting region.—GEO. D. FULLER.

Taxonomic notes.—BLAKE[15] has described a new variety of *Vernonia altissima* (*taeniotricha*) which occurs from Indiana and Illinois to Missouri and Mississippi.

BRITTON[16] has published a list of the Cuban species of *Rhynchospora*, with an analytical key. It is in Spanish and appears among the publications entitled "Memorias de la Sociedad Poey." The author lists 55 species, 6 of which are described as new.

BURT,[17] in continuation of his studies of North American Thelephoraceae, has monographed the genus *Coniophora*, recognizing 19 species, 5 of which are described as new.

DAVIE,[18] in connection with the publication of a list of plants collected in Brazil in 1914, has described new species in *Gaultheria* and *Pleurostachys*.

FERNALD,[19] in a series of short papers, has described new species and varieties in *Saxifraga* (province of Quebec) and *Vitis* (New England); also new varieties in various species of *Polygonum*, *Ranunculus* (4), *Anemone*, *Saxifraga*, *Cyperus*, *Stenophyllus*, and *Aster*.

FAWCETT and RENDLE[20] have described 3 new species of *Byrsonima* and a new *Zanthoxylum* from Jamaica.

HILL[21] has published a revision of the genus *Strychnos* in India and throughout the East. In that region he recognizes 91 species, 24 of which are described as new.

HEMSLEY[22] has described a new arborescent genus of Euphorbiaceae (*Riseleya*) from the Seychelles. It seems to be restricted to Mahé, where it was formerly common in the mountains.

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[15] BLAKE, S. F., Rhodora **19**:167. 1917.

[16] BRITTON, N. L., El genero *Rhynchospora* Vahl, en Cuba. Contrib. Jard. Bot. N.Y. no. 194. pp. 16. 1917.

[17] BURT, E. A., The Thelephoraceae of North America. VIII. *Coniophora*. Ann. Mo. Bot. Gard. **4**:237–269. *figs. 19.* 1917.

[18] DAVIE, R. C., Some Brazilian plants. Jour. Botany **55**:215–223. 1917.

[19] FERNALD, M. L., Contrib. Gray Herb. **19**:133–155. 1917.

[20] FAWCETT, W., and RENDLE, A. B., Notes on Jamaica plants. Jour. Botany **55**:268–271. 1917.

[21] HILL, A. W., The genus *Strychnos* in India and the East. Kew Bulletin, 1917: nos. 4 and 5. pp. 121–210.

[22] HEMSLEY, W. B., and TURRILL, W. B., Plants of Seychelles and Aldabra. Jour. Botany **55**:285–288. 1917.

HITCHCOCK and CHASE[23] have published a manual of all the known grasses of the West Indian Islands. The term "West Indies" is defined as including Bermuda, the Bahamas, Trinidad, and Tobago, but excludes the Dutch Islands off the coast of Venezuela. The publication contains descriptions of 455 species, representing 110 genera, including 17 new species and a new genus (*Saugetia*) related to *Gymnopogon*.

STEPHANI[24] has issued the fifth volume of his *Species Hepaticarum*, which deals with the Acrogynae, along with title page and index. He describes 296 species, chiefly established by himself, representing 16 genera, 9 of the species being new. The large genera are *Aneura* (113 spp.) and *Anthoceros* (64 spp.).

WERNHAM,[25] in continuation of his studies of tropical American Rubiaceae, has described 7 new species of *Psychotria*. The same author[26] has described 10 new species of *Palicourea* and 2 new species of *Cephaëlis* from tropical America, chiefly Colombia.—J. M. C.

Sap concentration and plant communities.—Having developed a method of determining the osmotic pressure of cell sap by a depression of the freezing point, HARRIS[27] has proceeded to investigate the tissue fluids of plants typical of the deserts of Jamaica[28] and Arizona,[29] of the mesophytic vegetation of temperate regions, and of the rain forests of Jamaica.[30] Aside from an interesting mass of data regarding the peculiarities of the cell sap of individual species, two generalizations stand out as important contributions to ecological science. They are to the effect that (1) there is a direct relationship between growth forms and sap concentration, as shown in the higher osmotic concentration of

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[23] HITCHCOCK, A. S., and CHASE, AGNES, Grasses of the West Indies. Contrib. U.S. Nat. Herb. **18**:261–471. 1917.

[24] STEPHANI, F., *Species Hepaticarum*. Vol. V. Acrogynae (pars quarta). Geneva. 1916.

[25] WERNHAM, H. F., Tropical American Rubiaceae. IX. Jour. Botany **55**:251–254. 1917.

[26] ———, Tropical American Rubiaceae. IX. Jour. Botany **55**:279–285. 1917.

[27] GORTNER, R. A., and HARRIS, J. ARTHUR, Notes on the technique of the determination of the freezing point of vegetable saps. Plant World **17**:49–53. 1914.

[28] HARRIS, J. ARTHUR, and LAWRENCE, J. V., Cryoscopic determinations on the tissue fluids of the plants of the Jamaican coastal deserts. BOT. GAZ. **64**:285–305. 1917.

[29] HARRIS, J. ARTHUR, et al., On the osmotic pressure of the juices of desert plants. Science N.S. **41**:656–658. 1915.

HARRIS, J. ARTHUR, and LAWRENCE, J. V., The cryoscopic constants of expressed vegetable saps as related to local conditions in the Arizona deserts. Physiol. Researches **2**:1–49. 1916.

[30] HARRIS, J. ARTHUR, and LAWRENCE, J. V., The osmotic concentration of the tissue fluids of Jamaican montane rain forest vegetation. Amer. Jour. Bot. **4**:268–298. 1917.

the fluids from the leaves of woody as compared with those from herbaceous plants, and (2) that the sap concentration shows a variation corresponding to the xerophytism of the plant community from which the fluids are obtained.

The importance of the latter relationship has been given emphasis in a paper which gives a summary of results concerning large and widely differing plant formations.[31] Here it is seen that the concentration of the cell sap of the woody plants varies from 11.44 atmospheres for that from the rain forest and 14.4 for that from mesophytic habitats to 24.97–30.05 atmospheres for the fluids of desert plants. Herbaceous plants from these same habitats show sap concentration values of 8.80, 10.41, and 15.15 atmospheres respectively. As might be expected, succulent halophytes show even higher concentrations, culminating, perhaps, in 49.7 atmospheres for *Batis maritima*. Curiously enough, the epiphytes of the rain forest show concentrations of a low order, such as 3.34–4.88 atmospheres for the epiphytic Orchidaceae from Jamaica and Florida.

These and other similar results are sufficient to demonstrate that in this line of investigation there has been found a means of expressing in a quantitative manner the sap properties of both large and small plant communities; hence not only must the results themselves be regarded as important, but a much higher value must be placed upon the introduction of a method which will tend to exactness in studies of the physiological plant geography.—GEO. D. FULLER.

Natal vegetation.—In advancing our acquaintance with the vegetation of South Africa, BEWS[32] has made a study of the species native to Natal according to RAUNKIAER'S life-forms, and has expressed the results in a biological spectrum for that part of South Africa. Some of the conspicuous features of the vegetation as shown by this analysis are the richness, manifest in more than 3000 species, and the small number of large phanerophytes which is far below the average in contrast with the abundance of lianas, chamaephytes, and geophytes. One of the interesting incidental features of the vegetation consists in the presence of stem succulents, all possessing a milky juice, as they belong to the *Asclepiadaceae* and *Euphorbiaceae*.

In a more recent paper, the same writer[33] has described the vegetation of the mountains forming the western boundary of Natal and reaching an altitude of 3400 m. The outline of the plant communities involved shows that grassland and scrub associations predominate. Of the latter, the one developed

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[31] HARRIS, J. ARTHUR, Physical chemistry in the service of phytogeography. Science N.S. **46**:25–30. 1917.

[32] BEWS, J. W., The growth forms of Natal plants. Trans. Roy. Soc. S. Africa **5**:605–636. 1916.

[33] ———, The plant ecology of the Drakensberg range. Annals Natal Museum **3**:511–565. 1917.

upon many of the steep slopes is termed "Fynbosch" and described as a sclerophyllous formation comparable to the chaparral of the United States. It is dominated by shrubs with needle and ericoid leaves, conspicuous among which are the genera *Cliffortia* (Rosaceae) and *Erica*, both represented by several species, and a large number of woody Compositae. In its undergrowth, bulbous plants abound. From it BEWS traces a double succession, one to the "bush" or forest, in which *Podocarpus* spp. and *Celtis Kraussiana* are the most abundant trees, the other to the mountain veld. The former is clearly leading to the climax type of tree vegetation developing only under the most favorable conditions of soil and exposure; but the succession in the latter instance does not seem clear, for the veld is apparently more xerophytic, although more extensive than the "Fynbosch."—GEO. D. FULLER.

Germination of tree seeds.—BOERKER[34] has carried on three series of greenhouse cultures to determine the effect of light, soil moisture, and soil texture upon the germination of the seeds of various forest trees. The cultures were extensive and the environmental factors rather carefully controlled. The variations in response are too numerous to be touched upon in a review, but some items of the summary show that it has not been possible to isolate the effect of single factors, as it is stated that shade accelerates germination and this acceleration is due to increase in soil moisture caused by decreased evaporation and transpiration. On the other hand, light is found to play absolutely no part in the germination of tree seeds. Similarly, the differentiation between the effects of soil moisture and soil texture has not been accomplished.

The reaction of different tree species to the different sets of conditions is interesting, and the results should be of practical service to foresters. The increase of length of tap and lateral roots in *Pinus ponderosa* with diminishing soil moisture content may be cited as one of the results. *P. ponderosa* growing in the Rocky Mountains produces smaller seeds that germinate more quickly than those from the same species grown upon the Pacific coast. Similar differences were found for local varieties of *Pseudotsuga taxifolia;* while in both species large seeds proved superior to small, both in higher germination percentage and in the size of the seedlings.—GEO. D. FULLER.

Law of the minimum.—HOOKER[35] gives an interesting discussion on the application of the law of the minimum, or limiting factors, to biological problems. He is perhaps fortunate, in so far as rigid application of the law is concerned, in drawing his early illustrations from simple chemical and physical processes, for it is rapidly becoming a question whether the law applies to plant

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[34] BOERKER, R. H., Ecological investigations upon the germination and early growth of forest trees. 8vo. pp. 89. *pls.* 5. Thesis Univ. Nebraska. 1916.

[35] HOOKER, D. H., Liebig's law of the minimum in relation to general biological problems. Science N.S. **46**:197–204. 1917.

activities as generally as or with anything like the rigidity assumed by some workers. The fact of vicarious conditions, or stimuli, renders the conception of limiting factors less definite. In some light requiring seeds, for instance, several things can be substituted for light, as salts, higher temperatures, acids, etc. To speak of the lack of sufficient light as a limiting factor to germination helps little. What should be learned is, what internal condition, or inhibitor, may any one of these factors act upon to initiate growth? The conception of an external condition as a limiting factor frequently leads physiologists to fail to examine the internal mechanism upon which that and other factors play to bring about a given result. The reviewer feels that the law of the minimum should be applied to biological problems with due realization of its limitations. —WM. CROCKER.

Vegetation of Pennsylvania.—A description of the vegetation of the western part of Pennsylvania, by CRIBBS,[36] is organized upon a physiographic basis, including the swamp, lake-forest, ravine-valley, river, and upland series. The plant succession in each series is outlined and the composition of the principal associations indicated. The upland forest serves to indicate the interesting position of the flora, partaking of the northern forms, as seen in *Pinus Strobus*, *Betula lutea*, and *B. lenta*, combined with such typically southern species as *Magnolia acuminata*. The dominant members of the climax forest are found to be *Fagus grandifolia*, *Castanea dentata*, *Quercus alba*, and *Acer rubrum*. With these are associated such others as *Tsuga canadensis*, *Magnolia acuminata*, *Liriodendron Tulipifera*, and *Tilia americana*.—GEO. D. FULLER.

Germination of spores.—BRIERLY[37] has done an interesting piece of work upon spore germination which he summarizes as follows: "The ripe ascospores of *Onygina equina* will germinate directly after a prolonged resting period, which may be curtailed or eliminated by a preliminary treatment of the spores with artificial gastric juice, but not by subjection to low temperatures. The full grown unripe ascospores and the chlamydospores will germinate immediately in the absence of digestive treatment." Demand for a rest period is common in seeds. Frequently the need for a rest period is imposed by the presence of seed coats. Likewise BRIERLY believes this need is imposed in this form by the presence of the spore coat.—WM. CROCKER.

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[36] CRIBBS, J. E., Plant associations of western Pennsylvania with special reference to physiographic relationship. Plant World **20**:97–120, 142–157. 1917.

[37] BRIERLY, WILLIAM B., Spore germination in *Onygina equina* Willd. Ann. Botany **31**:127–132. 1917.

VOLUME LXV NUMBER 4

THE

BOTANICAL GAZETTE

APRIL 1918

CARDUACEOUS SPECIES OF PUCCINIA[1]

I. SPECIES OCCURRING ON THE TRIBE VERNONIAE

H. S. JACKSON

This is the first of a proposed series of papers dealing with the species of *Puccinia* occurring on the Carduaceae. It is planned to discuss in separate articles the species recorded on the host genera included in the different tribes of the family. The series is the result of a study made in connection with the preparation, by the writer, of the manuscript of the species of *Puccinia* occurring on this family of hosts for *North American Flora*.

The number of species of *Puccinia* described from all parts of the world as occurring on members of the Carduaceae is very large, more than 300, and on account of the great variety of forms, and the close relationship and variability of the hosts which they inhabit, they offer a very interesting as well as difficult group for study by the uredinologist. In order to understand properly the forms occurring in North America, a study is being made so far as possible of all the described species. In order to bring together the present knowledge of the species occurring on closely related hosts, the forms recorded on the different tribes of the Carduaceae are being taken up separately.

Species of *Puccinia* are recorded on but three genera of the carduaceous tribe Vernoniae as limited by O. HOFFMANN in ENGLER and PRANTL'S *Die Pflanzenfamilien;* these are *Vernonia*, *Elephantopus*, and *Piptocarpha*. The two latter genera harbor 2 species

[1] Presented in part before the Botanical Society of America at Pittsburgh, January 1, 1918. Contribution from the Botanical Department of the Purdue University Agricultural Experiment Station.

each, while on the genus first mentioned 25 species are here recognized. All of the species, so far as known, are autoecious, although the full life history has been determined for only a few. There are a number of unconnected species of *Aecidium* and *Uredo* recorded which are not discussed in this account. While it is possible that some of the former may belong to heteroecious species, there is no supporting evidence available.

The large number of species occurring on *Vernonia* and the great variation in morphological characters and in life history which they exhibit are perhaps unparalleled on any other host genus in this group of rusts. When we consider, however, that the most important influencing factor in the evolution of the parasitic fungi, particularly in a group as highly specialized as the rusts, is undoubtedly that of the host, it is perhaps to be expected that a genus of hosts which includes an estimated number of 600 species, many of which show great variation, should harbor a large number of species of closely related parasites. The genus *Vernonia* occurs in both the Eastern and Western Hemispheres, over a wide range of latitude and under almost every conceivable condition of climate and range of elevation.

It is noticeable that the species of rusts under discussion are more numerous in the subtropical than in the temperate regions. For example, while but one species of *Puccinia* occurring on 9 species of *Vernonia* is known in the United States, 10 species occurring on 8 hosts are known from Guatemala and Costa Rica. Three host species, *V. patens*, *V. leiocarpa*, and *V. trifloscu*losa, harbor two species each in the latter region. There are 17 different species recognized from North America, of which 4 have been collected in Mexico, 5 in the West Indies, and 10 in Guatemala and Costa Rica; 8 are known from South America and 3 from the Eastern Hemisphere; 2 species only are indigenous to both North and South America.

All of the material in the Arthur herbarium at the Purdue University Agricultural Experiment Station and in the herbarium of the New York Botanical Garden has been available in making this study. In addition, a very remarkable collection of unidentified specimens made by Professor E. W. D. HOLWAY in Guatemala

and Costa Rica was loaned to the writer for study by Dr. J. C. ARTHUR, to whom the material was sent. Professor HOLWAY has also kindly furnished other material from his very extensive herbarium. A number of collections made by the late W. A. KELLERMAN in Guatemala have also been included in this study. Most of the type collections of previously described species have been examined. A few from South America and Africa have not been seen, as the original specimens are in European herbaria and on account of the present unsettled conditions are not available.

The writer is under great obligations to Dr. J. C. ARTHUR and to Professor E. W. D. HOLWAY for the loan of material at their disposal and for reading the manuscript of this paper. Acknowledgment is also gratefully made to the members of the staff of the botanical department of the Purdue University Experiment Station for assistance in the details of the work. The species described as new from Guatemala and Costa Rica are published jointly under the authorship of Professor HOLWAY and the writer. The descriptions and notes, however, were prepared entirely by the writer, and he assumes all responsibility for any errors which future investigations may bring to light.

KEY TO SPECIES

Teliospores smooth or appearing so, often obscurely rugose
- Teliospores colorless or light cinnamon brown, smooth
  - Teliospores uniformly thick, rarely slightly thickened above
    - Teliospores averaging more than 60μ in length
      - Aecia present in life history
        - Peridium present
          - Teliospores 12–18μ in width; urediniospores 19–22 by 23–34μ ..... 1. *P. Becki*
          - Teliospores 18–20μ in width; urediniospores unknown ..... 2. *P. membranacea*
        - Peridium wanting; urediniospores 23–28 by 29–34μ. 3. *P. erratica*
      - Aecia lacking in life history or unknown
        - O, II, III present; teliospores 16–24 by 56–80μ.. 4. *P. Arthuriana*
        - III only described; spores 20–27 by 45–70μ.... 5. *P. vernoniicola*
    - Teliospores averaging less than 60μ in length
      - Teliospores less than 40μ long..... 6. *P. Vernoniae-mollis*
      - Teliospores more than 40μ long
        - Occurring on *Vernonia*

O, II, III present in life cycle; urediniospore wall 1.5–2.5 μ.... 7. *P. insulana*

O, I, II, III present in life cycle; urediniospore wall 1–1.5 μ.... 8. *P. fraterna*

Occurring on *Piptocarpha*

Teliospores 19–27 by 35–58 μ..... 28. *P. Piptocarphae*

Teliospores 27–34 by 45–60 μ..... 29. *P. leptoderma*

Teliospores appreciably thickened above

Teliospores light brown; I and III known..... 9. *P. Le Testui*

Teliospores colorless; II and III known..... 10. *P. hyalina*

Teliospores dark cinnamon or chestnut brown, thickened at apex, frequently obscurely verrucose-rugose

Uredinia unknown; teliospores chestnut brown, narrowed below

Teliospores 20–25 by 45–50 μ..... 11. *P. vernoniphila*

Teliospores 15–17 by 40–50 μ (micro-form)..... 26. *P. paupercula*

Uredinia present; teliospores dark cinnamon or chestnut brown, rounded below

Urediniospore wall cinnamon brown

Urediniospore pores 4–6, scattered..... 12. *P. fuscella*

Urediniospore pores 2–3, approximately equatorial

Teliospores 20–28 by 30–45 μ..... 13. *P. Vernoniae*

Teliospores 21–30 by 40–60 μ..... 14. *P. Lorentzii*

Urediniospore wall colorless to faint golden brown 15. *P. semiinsculpta*

Teliospore wall prominently roughened

Uredinia with encircling paraphyses; teliospore markings tuberculate..... 16. *P. rata*

Uredinia without paraphyses

Teliospore markings verrucose or echinulate-verrucose

Uredinia or urediniospores present in life cycle

Markings of teliospore prominent and closely placed

Urediniospores ellipsoid to obovoid, 18–21 by 23–28 μ..... 17. *P. idonea*

Urediniospores globoid to obovoid, 22–26 by 26–32 μ..18. *P. notha*

Markings prominent, sparsely distributed

Urediniospore wall golden brown, thick; sori subepidermal 19. *P. egregia*

Urediniospore wall colorless, thin; sori deep seated..20. *P. praealta*

Uredinia and urediniospores unknown (micro-form)..27. *P. elephantopodis*

Teliospore markings rugose or verrucose-rugose

Telia gregarious or confluent (micro- or lepto-forms)

Teliospores not or slightly constricted..... 21. *P. rotundata*

Teliospores strongly constricted..... 22. *P. discreta*

Telia scattered; urediniospores present (hemi- or brachy-forms)

Teliospores averaging under 40 μ in length..... 23. *P. inaequata*

Teliospores averaging over 40 μ in length
Spores with abrupt semihyaline umbo at apex..... 24. *P. pinguis*
Spores rounded at apex
Urediniospores sparsely echinulate, 18–26 by 22–30 μ, wall 1.5–3 μ thick..... 15. *P. semiinsculpta*
Urediniospores closely echinulate, 26–29 by 29–34 μ, wall 3–3.5 μ thick..... 25. *P. Kuntzii*

1. PUCCINIA BECKI Mayor, Mem. Soc. Neuch. **5**:509. 1913.

O. Pycnia epiphyllous, few, gregarious on yellowish somewhat hypertrophied spots, 0.5–1 mm. across, frequently extending along veins, conspicuous, subepidermal, orange yellow, fading to blackish, globoid or flask-shaped, 112–120 by 125–130 μ, ostiolar filaments 50 μ long.

I. Aecia hypophyllous, few or solitary, in groups opposite the pycnia, cylindrical; peridium white, membranous, lacerate; peridial cells seen only in face view, irregularly polyhedral, 16–23 by 26–32 μ, wall colorless, thin, 1.5–2 μ, prominently verrucose-rugose; aeciospores globoid to ellipsoid, somewhat irregular, 16–22 by 23–34 μ, wall colorless, 2 μ thick, closely and prominently verrucose, with low warts often arranged in longitudinal lines, especially near either end, pores obscure.

II. Uredinia amphigenous, chiefly hypophyllous, scattered, small, 0.2–0.5 mm. across, round, early naked, somewhat pulverulent, cinnamon brown, ruptured epidermis not conspicuous; urediniospores globoid or broadly ellipsoid, 18–22 by 22–24 μ, wall pale cinnamon brown, about 2 μ thick, moderately echinulate, pores obscure.

III. Telia chiefly hypophyllous, scattered, small, 0.2–0.5 mm. across, round, early naked, compact, pulvinate, germinating at maturity, chestnut brown, ruptured epidermis not conspicuous; teliospores cylindrical or fusiform, 13–19 by 58–90 μ, wall cinnamon brown, 1–1.5 μ thick, smooth; pedicel colorless, fragile, short, up to 40 μ long.

On *Vernonia divaricata* Sw., I, II, III, Mandeville, Jamaica, February 23, 1915, *Holway*.

The collection from Jamaica already cited agrees in all essential features with the type of *P. Becki* in the uredinial and telial characters, and is assigned to that species with considerable confidence. In addition to the uredinia and

telia, the specimen bears mature aecia which without doubt belong in the life cycle, making it possible to complete the description. In the Arthurian classification this species would be assigned to the genus *Eriosporangium*. This species is known otherwise only from the type collection made by *Mayor* near Bogota, Department of Cundinamarca, Colombia, on *V. crotoneaster*.

2. PUCCINIA MEMBRANACEA Diet., Hedwigia **38**:251. 1899.

On *Vernonia cauloni* Sch., Tijuca, Rio de Janeiro, Brazil, May 1896, *E. Ule* 2337.

So far as can be determined from the literature, this species is known only from the type collection listed, which the writer has not seen. Only aecia and telia are described. It is evident from the description that it is closely related to the preceding species, although differing in the size of the aeciospores (25–30 by 30–35 μ) and in the width of the teliospores (18–20 by 60–90 μ), as well as in the absence of uredinia. The latter, however, in related rusts are often inconspicuous and sparingly developed and might easily be overlooked.

3. **Puccinia erratica** Jackson and Holway, nom. nov.—*Dietelia Vernoniae* Arth. BOT. GAZ. **40**:198. 1905; *Endophyllum Vernoniae* Arth. N. Am. Flora **7**:126. 1907.

O. Pycnia epiphyllous, numerous, in crowded groups, 1.0 mm. across, in the center of yellowish spots 0.5–1.0 cm. in diameter, conspicuous, subepidermal, orange becoming black, globose or flask-shaped, 120–145 by 145–160 μ, ostiolar filaments not extruded.

I. Aecia hypophyllous, few or solitary, crowded on the under side of yellowish spots opposite the pycnia or occasionally more or less scattered, bullate, 0.2–0.5 mm. across; peridium wanting; aeciospores somewhat irregularly ellipsoid, oblong or pyriform, 23–28 by 32–38 μ, somewhat flattened, wall colorless, 2–3 μ thick, prominently and closely verrucose-rugose, with a tendency to an arrangement in lines and uniting to form ridges at one end of the spore, tubercles often deciduous.

II. Uredinia hypophyllous, few, scattered, roundish, small, 0.1–0.3 mm. across, rather tardily naked, pulverulent, cinnamon brown, ruptured epidermis conspicuous; urediniospores globoid or broadly obovate, 23–28 by 29–34 μ, wall cinnamon brown, 1–1.5 μ, moderately echinulate, pores 3, approximately equatorial.

III. Telia hypophyllous, numerous, scattered or gregarious, round, small, 0.2–0.5 mm. across, early naked, pulvinate, chestnut brown, ruptured epidermis noticeable; teliospores cylindrical terete

or fusiform, 16–22 by 56–80 μ, narrowed at both ends, apex obtuse, not thickened, slightly constricted, wall cinnamon brown, thin, 1–1.5 μ, smooth, pedicel colorless, fragile, equaling the spore in length or usually shorter.

On *Vernonia Schiedeana* Less., Guatemala City, Guatemala, February 8, 1917, *Holway* 841, February 15, 1916, O, I, II, III, *Holway* 494; Chinautla, Guatemala, February 12, 1916, O, I, II, III, *Holway* 480; Moran, Dept. Amititlan, Guatemala, December 22, 1916, I, II, III, *Holway* 621; Cordoba, Vera Cruz, Mexico, January 27, 1895, O, I, II, III, *Pringle* 6080, from specimen in the phanerogamic herbarium of the New York Botanical Garden; Jalapa, Vera Cruz, Mexico, October 2, 1898, I, II, III, *Holway* 3111 (type of *Dietelia Vernoniae* Arth.).

In the course of the study of these collections it was at first thought that some of the specimens represented a mixture of *Endophyllum Vernoniae* and *Argomyces Vernoniae* (cf. 7), the aecia agreeing in morphology with the former and the uredinia and telia closely resembling the latter. A most careful examination, however, failed to reveal the presence of pycnia associated with the uredinia in any of the collections, and a re-examination of the type of *Endophyllum Vernoniae* showed a few telial sori and a few urediniospores which agree with those of the other collections. All of the collections cited show all spore stages of the rust and the association cannot be interpreted as accidental. The rust, according to this interpretation, is of the *Eriosporangium* type, possibly a correlated form with *Argomyces Vernoniae*. It is evidently closely related to the two preceding, differing, however, in the absence of a typical peridium in the aecia.

The Cordoba collection differs from the Guatemalan material in the somewhat broader teliospores, a greater proportion of which are shorter than the maximum measurements given. The aecia are usually solitary and occur on noticeably thickened areas rather than on yellowish spots as in most of the Guatemalan collections. The material is scanty, however, and the leaves are evidently from a more mature, less vigorously growing specimen of the host than the other collections.

4. **Puccinia Arthuriana,** nom. nov.—*Argomyces Vernoniae* Arth. N. Am. Flora 7:218. 1912, not *P. Vernoniae* Schw. 1832.

On *Vernonia arbuscula* Less., II, Pineland, Long Bay Cays Section, Andros, Bahamas, January 20–22, 1910, *J. K. Small* and *J. J. Carter* 8613; *Vernonia bahamensis* Griseb., II, III, North Caicos, Bellemont and vicinity, Bahamas, March 2, 1911, *C. F.* and *C. M. Millspaugh* 9175; II, Whiteland, Tenados, Inagua, Bahamas, October 28, 1904, *G. V. Nash* and *N. Taylor* 1344; II, Hanna Hill, Long Cay, Bahamas, December 7–17, 1905, *L. C. K. Brace* 4020; *Vernonia canescens* H.B.K., II, III, Volcan de Irazu, Cartago, Costa Rica,

December 24, 1915, *Holway* 281; San José, Costa Rica, January 3, 1916, O, II, III, *Holway* 360.

This species has previously been recorded only from Porto Rico,[2] on *V. albicaulis*, *V. borinquensis*, and *V. sericea* (*V. phyllostachya*). The specimen from St. Croix, listed with the original description, has since been referred to *Puccinia* (*Argomyces*) *insulana* (cf. 7). All but the last mentioned collections are from phanerogamic specimens in the herbarium of the New York Botanical Garden, obtained by the writer in January 1917. All are previously unrecorded hosts.

5. PUCCINIA VERNONIICOLA P. Henn. in Engler, Pfl. Ost.–Afr. C:50. 1895.

On *Vernonia* sp., Marangu, Africa, *Volk* 2257.

This species has not been seen by the writer and apparently has been recorded only from the type locality noted. Only telia and teliospores are described. SYDOW[3] has evidently redescribed this from authentic material and his description of the sori (sparsis, rotundatis, 2–2.5 mm. diam., pulvinatis) would suggest that it is a lepto-*Puccinia* and not to be confused with any form yet recorded from North America.

6. PUCCINIA VERNONIAE-MOLLIS Mayor, Mem. Soc. Neuch. 5:510. 1913.—*Aecidium Vernoniae-mollis* Mayor, Mem. Soc. Neuch. 5:570. 1913.

This species was described from material collected by MAYOR in the central Andes, Dept. Antioquia, Colombia, on *Vernonia mollis* (?). Four collections of uredinia and telia were made, two of which correspond in data of place and date with collections of aecia on the same host described separately. Judging from the description of the aecia (only uredinia and telia having been seen by the writer), it would seem probable that the aecia belong in the life history as they appear to be of a type common in this group of rusts. If this surmise is correct, this species is of the *Eriosporangium* type. The matter is complicated by the fact that MAYOR made two collections of another uredo (*U. Vernoniae* Mayor) on the same host, one of which corresponds in data with one of the aecial collections. As pointed out by MAYOR, the final disposition of the various forms can be made only on more extended field observations or cultures. This species differs from all other related rusts on *Vernonia* in the small size of the teliospores (14–21 by 30–38 μ).

7. **Puccinia insulana** (Arth.), comb. nov.—*Argomyces insulanus* Arth. Mycologia 7:179. 1915.

[2] ARTHUR, J. C., Mycologia 7:180. 1915; 8:24. 1916; 9:67. 1917.

[3] Monographia Uredinearum 1:177. 1902.

On *Vernonia divaricata* Sw., Oxford, Jamaica, September 13–18, 1906, *N. L. Britton* 431; Hillside, Blue Fields Mountain, Jamaica, March 6–7, 1908, *N. L. Britton* and *A. Hollick* 1996; *Vernonia longifolia* Pers., Antigua, West Indies, February 6, 1913, *J. N. Rose* et al. 3291; *Vernonia* sp., Retalhuleu, Guatemala, February 26, 1916, *Holway* 537.

This very distinct brachy-form was originally described from Porto Rico and St. Croix on *V. albicaulis* (*l.c.*) and on *V. longifolia* from Porto Rico. The above collections, excepting the last, were obtained from an examination of phanerogamic specimens in the herbarium of the New York Botanical Garden and, besides adding a new host for the species, extends the range to include Jamaica, Antigua, and Guatemala.

8. **Puccinia fraterna,** sp. nov.

O. Pycnia epiphyllous, few, gregarious, noticeable, subepidermal, blackish, globose, 110–120 μ in diameter, ostiolar filaments not protruding.

I. Aecia hypophyllous, few, crowded in small groups, opposite the pycnia, bullate, 0.2–0.5 mm. across; peridium short cylindrical, white, lacerate; peridial cells rectangular, abutted or slightly overlapping, 10–12 by 26–35 μ, wall colorless, outer wall smooth, 1.5 μ thick, inner very closely verrucose, 4 μ thick; aeciospores globoid or broadly ellipsoid, 18–23 by 23–32 μ; wall colorless, 1–1.5 μ thick, closely and finely verrucose.

II. Uredinia hypophyllous, few, scattered, small, 0.2–0.5 mm. across, pulverulent, cinnamon brown, ruptured epidermis not conspicuous; urediniospores broadly ellipsoid or obovate, 23–26 by 26–32 μ; wall pale cinnamon brown, 1–1.5 μ thick, moderately echinulate, pores 2 or 3, equatorial.

III. Telia hypophyllous, few, scattered, small, 0.2–0.5 mm. across, early naked, chestnut brown, ruptured epidermis not conspicuous; teliospores fusiform or oblong fusiform, 19–26 by 44–60 μ, narrowed above and below, somewhat constricted, wall cinnamon brown, uniformly 1 μ thick, smooth; pedicel colorless, fragile, about half the length of the spore.

On *Vernonia pluvialis* Gleason, Summit Blue Mt. Peak, Jamaica, July 24, 1903, O, I, II, III, *G. E. Nichols* 120 (type); May 14, 1906, O, I, *Forrest Shreve*.

The specimens on which this species is based were obtained from phanerogamic specimens in the herbarium of the New York Botanical Garden. The first collection mentioned bears all stages of the rust; the other, found on the type specimen of the host species, bears pycnia and aecia only. The material

is fragmentary and admitting of rather incomplete description of some stages. The species, however, is clearly distinct from any form previously described, having medium sized teliospores and possessing aecia with peridia. It is apparently most closely related to *P. insulana*, and difficult to separate from it in the uredinial and telial characters. The urediniospores, however, have thinner walls and the teliospores are somewhat narrower. The presence of aecia, however, clearly distinguishes it from that species. It should doubtless be considered a correlated form.

9. PUCCINIA LE TESTUI Maubl. Bull. Soc. Myc. Fr. **22**:71. 1906.

This species is known only from Marromen, East Africa, on *Vernonia* sp. No material has been available for study. Aecia and telia only are known, the latter described as oblong to ellipsoid-oblong, apex rounded, base narrowed, constricted at the septum, wall thick, apex thickened to 8 μ, papillate, smooth, "flavo-brunneis," 18–25 by 36–50 μ, pedicel subhyaline. persistent, to 50 μ long. From this it would appear to be different from any other described species, although possibly close to *P. fuscella*.

10. **Puccinia hyalina,** sp. nov.

O and I. Pycnia and aecia unknown.

II. Uredinia amphigenous, scattered, occasionally gregarious, roundish, 0.2–0.4 mm. across, tardily naked, pulverulent, cinnamon brown, ruptured epidermis conspicuous; urediniospores broadly ellipsoid or obovoid, 22–26 by 29–34 μ, wall dark cinnamon brown, 1.5–2.5 μ thick, strongly and sparsely echinulate; pore one, basal, near the hilum.

III. Telia hypophyllous, scattered or gregarious, round, small, 0.2–0.4 mm. across, early naked, pulvinate, whitish or cinereous, ruptured epidermis not conspicuous; teliospores ellipsoid or obovoid, 18–22 by 36–46 μ, rounded at apex and base or narrowed below, slightly constricted, germinating at maturity; wall colorless, thin, 1 μ, thickened at apex to 6–8 μ, smooth; pedicel colorless, equaling the spore.

On *Vernonia scariosa* Arn., Ceylon, April 23, 1915, *T. Petch.*

A very distinct species, easily separated from all other rusts on *Vernonia* by the single basal pore of the urediniospore and the colorless teliospores appreciably thickened at the apex.

11. PUCCINIA VERNONIPHILA Speg. Ann. Mus. Buenos Aires **19**:306. 1909.

Only one collection of this species has been recorded, on *V. flexuosa* from Buenos Aires, November 1907. No material has been available for study, and its relation to the other species cannot be stated with any degree of accuracy. Telia only are described, the spores being "obscure fusco-ferrugineae superne obtusae inferne subcuneatae (20–25 by 45–50 μ) . . . . non v. leniter constrictae, episporio ad vesticem sat incrassato." The description of the sori would not suggest a micro- or lepto-form, and it is probable that other stages exist.

12. PUCCINIA FUSCELLA Arthur and Johnston, Mem. Torr. Bot. Club 157. 1918.

On *Vernonia menthaefolia* Less., El Yunque Baracoa, Cuba, March 10, 1903, *E. W. D. Holway;* Baracoa, April 14, 1916, *J. R. Johnston* 584 (type).

This species has formerly been confused with *P. Vernoniae* Schw. (cf. 13). It differs, however, in well marked characters, especially in the distribution of the pores in the urediniospores, which are 4–6 and scattered, while in *P. Vernoniae* they are 3 and equatorial. The species is known only from Cuba. The first mentioned specimen was issued as no. 772 in Barth. N. A. Ured. as on *V. longifolia.*

13. PUCCINIA VERNONIAE Schw. Proc. Am. Phil. Soc. II. **4**:296. 1832.—*P. bullata* Schw. Schrift. Nat. Gesell. Leipzig **1**:74. 1822; not *P. bullata* Lk. 1815 or Schroet. 1879; *P. tanaceti Vernoniae* Burr. Ill. Lab. Nat. Hist. **2**:186. 1885; *P. Vernoniae longipes* Diet. Jour. Mycol. **7**:43. 1891; *P. Vernoniae brevipes* Diet. Mycol. **7**:43. 1891; *P. longipes* Lagerh. Tromsö Mus. Aarsh. **17**:64. 1895; *Dicaeoma longipes* Kuntze, Rev. Gen. **3**:469. 1898; *Bullaria Vernoniae* Arth. Mycol. **9**:302. 1917.

O. Pycnia epiphyllous, few, scattered among the uredinia, small, punctiform, subepidermal, honey yellow, becoming brown, globose, 112 μ in diameter by 120–130 μ in height; ostiolar filaments free.

II. Primary uredinia chiefly epiphyllous, rather numerous, crowded in groups up to 4 mm. in length, often confluent, small, round, 0.3–0.5 mm. across, rather early naked, pulverulent, cinnamon brown, ruptured epidermis inconspicuous; secondary uredinia amphigenous, often gregarious like the primary on yellow spots, or more often scattered, small, 0.2–0.5 mm. across, ruptured epidermis often conspicuous; urediniospores obovoid or broadly ellipsoid, 20–26 by 22–30 μ; wall cinnamon brown, 1.5–3 μ thick, moderately to sparsely and prominently echinulate; pores 3, approximately equatorial.

III. Telia amphigenous and caulicolous, on the leaf blades often gregarious or confluent, in groups of 0.5–1.5 mm., more often scattered, round, 0.2–0.5 mm. across, on the stems fusiform, 10–30 mm. long; early naked, becoming somewhat pulverulent, dark chocolate brown, ruptured epidermis noticeable when epiphyllous, inconspicuous when hypophyllous; teliospores oblong or ellipsoid, often irregular, 20–28 by 30–45 μ, somewhat longer and narrower in caulicolous sori, 19–26 by 40–58 μ, obtuse or rounded above, rounded or narrowed below, slightly or not constricted at septum (more frequently so in caulicolous form); wall light chestnut brown, minutely verrucose, often appearing smooth, medium thick, 1.5–3 μ, thicker at apex, 5–10 μ, concolorous or often slightly lighter above; pedicel colorless, slender, once to twice the length of the spore, in the caulicolous form usually much longer.

On *Vernonia altissima* Nutt. (*V. maxima* Small), Indiana, Michigan; *V. Baldwinii* Torr. (*V. interior* Small), Illinois, Kansas, Michigan, Nebraska, Oklahoma; *V. crinita* Raf., Arkansas, Michigan; *V. Ervendbergii* Gray, San Luis Potosi; *V. fasciculata* Michx., Illinois, Iowa, Michigan, Nebraska, North Dakota, Oklahoma, South Dakota; *V. gigantea* (Walt.) Britt., Texas; *V. guadalupensis* Heller, Texas; *V. missourica* Raf. (*V. Drummondii* Shuttlw.), Missouri; *V. noveboracensis* (L.) Willd., Delaware, Illinois, Iowa, North Carolina; *V. pulchella* Small, Georgia; *V.* sp., Virginia.

Type locality: Salem, North Carolina, on *Vernonia noveboracensis*.

Exsiccati: Sydow Ured. 273, 1015; Ellis and Ev. N. A. Fungi 1847, 2988, 3050; Ellis and Ev. Fungi Columb. 263, 353, 1670, 1774; Barth. Fungi Columb. 2573, 2970, 3271, 3674, 4276; Barth. N. A. Ured. 69, 70, 578, 873, 874, 973; Brenckle, Fungi Dakot. 369; Seym. and Earle, Econ. Fungi Suppl. B 20.

This very common species is apparently confined to the United States, and the only one so far recorded north of Mexico. The name first proposed by SCHWEINITZ was based on collections made at Salem, North Carolina, occurring "erumpent from the dried stems of various plants, e.g. *Ambrosia*, *Chenopodium*." In his later publication he cites it as occurring in Pennsylvania on *V. noveboracensis*. An examination of the material in the Schweinitz collection at the Philadelphia Academy of Science made by ARTHUR, shows that there are three packets, containing in the aggregate 9 pieces, of similar stems bearing large sori up to 3 cm. long. The original packet reads "*P. bullata* LvS. Salem and Beth. in caulibus varies." The stems all appear to be of *Vernonia*, and the rust when examined microscopically does not differ from similar material on *Vernonia* stems (now interpreted as *V. altissima*) collected by UNDERWOOD at Fern, Putnam County, Indiana, and distributed in Ellis and Ev. N. A. Fungi (2988) and other exsiccati under the name *P. Vernoniae*

Schw. No other rust with which this could possibly be confused is known to occur on the stems of *Ambrosia* or *Chenopodium*, or on any other host within the range of this species.

LAGERHEIM based his *P. longipes* on material of *P. bullata* Schw. in the E. Fries herbarium, communicated by SCHWEINITZ, said to be on culms or petioles of *Ambrosia* sp.

DIETEL (*l.c.*) based his varieties on supposed differences in the length of the pedicel in this rust on different hosts, a difference which is not borne out by an examination of the large series of specimens in the Arthur herbarium.

That the rust on the stems is the same as the more common, or at least more frequently collected, form on the leaves has been shown by ARTHUR, who, in 1916 (Mycol. **9**:302, 1917), using telial material from the stems of *Vernonia* sp. collected by C. H. CRABILL at Cliffview, Va., and communicated by F. D. FROMME, succeeded in obtaining the development of pycnia and uredinia on the leaves of *Vernonia* sp. This culture also demonstrates that this rust, whose life history has long been in doubt, is a brachy-form referable to the genus *Bullaria*. Pycnia have not been observed in any field collections thus far studied.

14. PUCCINIA LORENTZII P. Henn. Hedwigia **35**:239. 1896.

The type of this species was collected by LORENTZ in Argentina, February 1878, on *Vernonia Lorentzii* Hieron. It is also recorded from the same region on *V. mollissima* and from Brazil on *V. scorpioides*. The only specimen recorded by HENNINGS, which has been seen by the writer, is presumably the collection which he records as on *Vernonia* sp. made by *E. Ule* (1414) in Sta. Cathrina pr. Tubarao, Brazil. The specimen examined is from the herbarium of E. W. D. HOLWAY and agrees with the data given by HENNINGS, except that the host is *V. scorpioides* and the number 1441. This specimen bears uredinia only, and the spores, as stated by HENNINGS, differ slightly from those of the other collections. The spores are ellipsoid to obovoid, 23–24 by 26–32 μ, wall cinnamon brown, 1.5–2 μ thick, minutely and moderately echinulate, the pores 3, equatorial. Another specimen distributed by VESTERGREN (Micromycetes rariores selecti 1289), collected by *Rob. E. Fries* in Prov. Jujuy, Argentina, on *V. scorpioides*, has been examined and found to bear uredinia only, the spores being similar to the *Ule* collection. In the absence of other material for examination it is possible that the assignment in the preceding key is incorrect.

15. PUCCINIA SEMIINSCULPTA Arth. BOT. GAZ. **40**:204. 1905.

O. Spermogonia epiphyllous, few in small groups, punctiform, honey yellow becoming brown, immersed, subepidermal, globose, 150–180 μ across.

II. Primary uredinia epiphyllous, surrounding the pycnia on yellowish hypertrophied spots with purple border, secondary scattered, round, small, 0.2–0.3 mm. across, soon naked, pale cinnamon brown, pulverulent, ruptured epidermis noticeable; urediniospores broadly ellipsoid, obovoid, or globoid, 18–26 by 22–30 μ; wall golden yellow fading to nearly colorless, medium thick, 1.5–3 μ, sparsely and evenly echinulate, pores indistinct, 2–3 and equatorial.

III. Telia amphigenous, or often only epiphyllous, scattered, round, small, 0.2–0.5 mm. across, often confluent, soon naked, chocolate brown, compact and cinereous from germination or pulverulent, ruptured epidermis inconspicuous; teliospores elliptical or elliptical-obovate, 22–38 by 38–50 μ, rounded above, rounded or somewhat narrowed below, slightly or not constricted at septum; wall finely to coarsely reticulate-verrucose with irregular, crowded sculpturing, golden brown in the germinating form to chocolate brown in the pulverulent form, 3–6 μ thick, slightly or not thicker at apex, 4–10 μ, much thinner at base in the germinating form; pedicel colorless, rather slender, 5–9 μ thick, once to twice length of spore, minutely rugose, or nearly smooth.

On *Vernonia Alamani* DC., Amecameca, Mexico (state), October 31, 1899, *Holway* 3754 (type), distributed in Barth. Fungi Columb. 4573; October 30, 1903, *Holway* 5190, distributed in Barth. N. A. Ured. 168; Oaxaca, November 11, 1903, *Holway* 5379; Patzcuaro, Michoacan, October 13, 1899, *Holway* 3631; October 10, 1899, *Holway* 3602; October 17, 1898, *Holway* 3105; *V. Karwinskiana* DC., Las Sedos, Oaxaca, Mexico, October 30, 1894, *C. G. Pringle* 6019; *V. umbellifera* Gleason, Guadalajara, Jalisco, Mexico, October 16, 1889, *C. G. Pringle* 2316; *Vernonia* sp., Oaxaca, Mexico, October 18, 1899, *Holway* 3668, distributed in Barth. N. A. Ured. 1570; Chapala, Mexico, September 19, 1899, *Holway* 5459; Cuernavaca, Mexico, September 30, 1899, *Holway* 3540; Morelos, Mexico, September 8, *Arsène* (Field Museum, sheet 386949).

This remarkable species presents some puzzling features. The teliospores, as stated in the description, are of two forms, quite different in general characters. The thin-walled, lighter colored spores are often found in a germinating condition. The thick-walled, darker spores show no evidence of germination. All gradations between the extremes of the two forms may be found in the same collection and even in the same sorus. It is possible that this species should be regarded as indicating a transitional relation between the *Argomyces* type and the usual form.

The species as here considered follows closely the original interpretation of ARTHUR. It should be noted that certain collections (*Holway* 3459, 3668) show only the thick-walled form, and the sori are chiefly epiphyllous, while in the typical form the sori are chiefly hypophyllous. The two *Pringle* collections add new hosts for the species. The first mentioned was obtained through the courtesy of HOLWAY, the other from a phanerogamic specimen in the herbaria of the New York Botanical Garden and of the Field Museum (sheets 104882, 262977).

16. **Puccinia rata** Jackson and Holway, sp. nov.

O and I. Pycnia and aecia unknown.

II. Uredinia amphigenous, chiefly hypophyllous, scattered, round, standing out from surface of leaf, small, 0.2–0.4 mm. across, early naked, becoming pulverulent, cinnamon brown, epidermis not conspicuous; surrounded by abundant encircling paraphyses, standing well out from substratum, paraphyses incurved, clavate, 15–18 by 100–125 μ, wall colorless or very slightly tinted with brown, uniform, thin, 0.5–1 μ; urediniospores globoid or broadly obovate, 24–29 by 26–32 μ; wall dark cinnamon brown, 2.5–3.5 μ thick, rather closely echinulate; pores 4–5, scattered.

III. Telia hypophyllous, scattered or gregarious, round, small, 0.2–0.4 mm. across, early naked, becoming pulverulent, early formed sori surrounded by paraphyses like the uredinia, later formed sori without paraphyses; teliospores broadly ellipsoid, 26–30 by 32–42 μ, rounded at both ends, slightly or not constricted at septum; wall uniform, chestnut brown, 3.5–5 μ thick, thickened to 5–7 μ at apex and over pore of lower cell, which is usually placed half way from pedicel to septum, prominently and evenly tuberculate with closely set low tubercles, 1 μ in height, having polygonal bases; pedicel short, 5–10 μ, colorless, deciduous.

On *Vernonia leiocarpa* DC., Guatemala City, Guatemala, February 13, 1916, II, III, *Holway* 490 (type); February 15, 1916, II, III, *Holway* 495a; March 17, 1916, II, III, *Holway* 585; Mendez, Dept. Guatemala, February 13, 1917, *Holway* 860; Antigua, Dept. Sacatepequez, February 4, 1907, *Kellerman* 6300.

Known only from Guatemala, this very distinct species is easily separated from all others on *Vernonia*, studied by the writer, in the presence of abundant paraphyses with the uredinia and in the tuberculate markings of the teliospores. It is accompanied on some of the collections (*Holway* 495a, *Kellerman* 6300)

by another species, *P. notha* (18), from which it is, however, readily distinguished by well marked characters. In *P. notha* the uredinia are not accompanied by paraphyses and the spores are colorless. The teliospores, while similar to the present species in shape and size, have verrucose markings and long pedicels. In *P. rata* the sori are in general hypophyllous, while in *P. notha* they are characteristically epiphyllous on the specimens examined.

17. **Puccinia idonea** Jackson and Holway, sp. nov.

O and I. Pycnia and aecia unknown.

II. Uredinia amphigenous, scattered or somewhat crowded and frequently confluent along the midribs and larger veins, roundish or somewhat elongated, 0.3–0.6 mm. across, early naked, pulverulent, lemon yellow fading to white, ruptured epidermis conspicuous; urediniospores broadly ellipsoid or obovoid, 18–21 by 23–28 μ, wall colorless, thin, 1–1.5 μ, finely and moderately echinulate, the pores obscure but apparently equatorial.

III. Telia amphigenous, chiefly hypophyllous, scattered or somewhat crowded and frequently confluent along the midribs and larger veins, roundish or somewhat elongated 0.3–0.6 mm. across, early naked, pulvinate becoming pulverulent, blackish brown, ruptured epidermis conspicuous; teliospores broadly ellipsoid, 23–28 by 35–45 μ, rounded at both ends, not or scarcely constricted, wall chestnut brown, medium thick 3–4 μ, slightly thickened at apex and over pore of lower cell to 7 μ, prominently and evenly verrucose with broad low projections rather closely set, sometimes arranged in lines; pedicel colorless, flexuous, twice the length of the spore, 3–5 μ thick, transversely rugose at base and swelling slightly.

On *Vernonia trifloscula* H.B.K., San Jose, Costa Rica, January 8, 1916, *Holway* 398; January 18, 1916, *Holway* 445; Chinaulta, Dept. Guatemala, February 12, 1916, II, III, *Holway* 481; Esquintla, Guatemala, February 17, 1916, II, III, *Holway* 498, 499, type; Panajachel, Dept. Solola, Guatemala, January 3, 1917, II, III, *Holway* 670.

This species occurs on the same host and from the same region as *P. praealta* (cf. 20), but differs in the character of the sori as well as in microscopic characters. It is perhaps most closely related to the next described species. The urediniospores, however, are narrower and shorter, with little or no tendency to be globoid. The teliospores in this species, while similar in size and shape, have markings which are less pointed and hence nearly hemispherical and somewhat more closely placed. The pedicel has a tendency to swell slightly

at the base, while in the latter it is attenuated. The uredinia in gross appearance resemble those of *Coleosporium*. The spores, however, are echinulate and borne on pedicels, and sections show urediniospores and teliospores in the same sorus.

18. **Puccinia notha** Jackson and Holway, sp. nov.

O. Pycnia epiphyllous, few, gregarious, inconspicuous, subepidermal, depressed globoid or conical, 60–90 by 50–90 μ, ostiolar filaments short.

I. Aecia hypophyllous, few, gregarious on somewhat thickened spots, peridium cylindrical, whitish, membranous, rupturing irregularly, peridial cells seen only in face view, irregularly polyhedral or rectangular, 18–26 by 35–48 μ, wall colorless, thin, 1–2 μ, closely verrucose-rugose; aeciospores somewhat irregularly ellipsoid or globoid, 20–26 by 26–35 μ, wall thin 1–1.5 μ, closely verrucose, markings somewhat deciduous, pores not evident.

II. Uredinia amphigenous, few, scattered, round, very small, 0.1–0.2 mm. across, early naked, pulverulent, whitish, ruptured epidermis not conspicuous; urediniospores globoid or obovoid, 22–26 by 26–32 μ; wall colorless, 1.5–3 μ thick, moderately echinulate; pores obscure.

III. Telia amphigenous, chiefly epiphyllous, scattered or gregarious, small, 0.2–0.8 mm. across, early naked, becoming pulverulent, blackish brown, ruptured epidermis not conspicuous; teliospores broadly ellipsoid, 26–34 by 35–48 μ, rounded at both ends, slightly or not constricted, wall chestnut brown, 3.5–5 μ thick, slightly thickened by a subhyaline umbo to 7 μ at apex and over pore of lower cell which is usually placed near pedicel or half way between pedicel and septum, prominently, evenly and moderately verrucose, with acute points about 3–4 μ apart; pedicel colorless, persistent, firm, once to two and a half times the length of the spore, 5–7 μ thick, tapering and minutely verrucose at the lower end, often attached laterally.

On *Vernonia leiocarpa* DC., San Rafael, Guatemala, January 7, 1915, *Holway* 21; Solola, 7000 ft., January 28, 1915, I, II, III, *Holway* 148 (type); Antigua, February 4, 1907, *Kellerman* 6300a; Volcan de Agua, Antigua, March 4, 1916, II, III, *Holway* 550; Guatemala City, February 15, 1916, III, *Holway* 495; March 17, 1916, III, *Holway* 585a; Huehuetnango, January

21, 1917, I, II, III, *Holway* 759; Quezaltenango, January 16, 1917, I, II, III, *Holway* 732; *V. Shannoni* Coulter (?), Quezaltenango, January 31, 1917, *Holway* 814.

Known only from the above mentioned collections from Guatemala. As previously noted (cf. 16), this species is often accompanied on the same leaves with *P. rata*, from which it differs in well marked characters. It is closely related to *P. idonea* (cf. 17) and perhaps to *P. egregia* (cf. 19). In the Quezaltenango collection (732) the teliospores have much shorter pedicels than in the other collections, and the sori are equally abundant on both surfaces of the leaf, instead of being chiefly epiphyllous as in all the other collections examined.

19. PUCCINIA EGREGIA Arth. BOT. GAZ. **40**:204. 1905.

II. Uredinia not seen; urediniospores from telial sori globoid or obovoid, 23–26 by 24–28 μ; wall golden yellow, medium thick, 1.5–2.5 μ, moderately echinulate; pores obscure, apparently 3 equatorial.

III. Telia amphigenous, scattered, round, 0.2–0.5 mm. across, early naked, pulvinate, becoming somewhat pulverulent, chocolate brown, ruptured epidermis inconspicuous; teliospores broadly ellipsoid, 26–30 by 35–45 μ, rounded at both ends, not constricted at septum; wall chestnut brown, very thick, 4–6 μ, very slightly thickened at apex and over pore of lower cell, the latter placed near the pedicel, uniformly coarsely and prominently verrucose with conical and well separated papillae; pedicel slender, 4–6 μ thick, once to twice the length of the spore or occasionally longer, wall thin, smooth, colorless.

On *Vernonia uniflora* Schz. Bip.

Known only from a single collection, obtained from a phanerogamic specimen in the herbarium of the New York Botanical Garden, on *V. uniflora*, collected at Oaxaca, Mexico, December 29, 1895, by *Seler* (1739). The material is very meager and admits of but incomplete description. It is, perhaps, very closely related to *P. notha* (cf. 18), from which it differs in the somewhat more prominent, very sparsely distributed, rather more sharply pointed markings on the teliospore wall. The urediniospore wall is golden yellow instead of colorless, as in *P. notha*.

20. **Puccinia praealta** Jackson and Holway, sp. nov.

O and I. Pycnia and aecia unknown.

II. Uredinia epiphyllous, densely gregarious and often confluent on irregular spots, 0.5–2 mm. across, bullate, 0.2–0.4 mm. across, long covered by the overarching and conspicuous epidermis, deep

seated, arising from below the palisade layer, pulverulent, light yellow fading to whitish; urediniospores ellipsoid or obovoid, 18–20 by 24–28 μ, wall pale yellow or colorless, thin, 1–1.5 μ, finely and moderately echinulate, pores obscure, apparently 2 equatorial.

III. Telia epiphyllous, densely gregarious and often confluent on irregular spots, 0.5–1.5 mm. across, becoming scattered, bullate, 0.2–0.4 mm. across, long covered by the overarching and conspicuous epidermis, deep seated, arising from below the palisade layer, compact, chestnut brown; teliospores ellipsoid, 24–28 by 32–40 μ, rounded at both ends, slightly or not constricted at septum, wall light chestnut brown, 3–4 μ thick, slightly thickened over the pore of either cell, 4–5 μ, rather prominently and sparsely verrucose, with conical projections; pedicel colorless, once to twice length of spore.

On *Vernonia trifiosculosa* H.B.K., Mazatenango, Guatemala, February 21, 1916, *Holway* 510 (type); San Jose, Costa Rica, II, III, January 10, 1916, *Holway* 407; San Ramon, Costa Rica, January 13, 1916, II, *Holway* 426; Heredia, Costa Rica, December 17, 1915, II, *Holway* 262.

A very distinct species, separable from all others on *Vernonia* by the very deep seated, strictly epiphyllous sori, arising from beneath the palisade layer of leaf tissue. The sori are aggregated in definite groups, presenting the appearance, on cursory examination, of a micro-form. It is quite different from *P. idonea* (cf. 17), which occurs on the same host from the same region.

21. PUCCINIA ROTUNDATA Diet. Hedwigia **36**:32. 1897.—*P. rugosa* Speg. Ann. Soc. Cient. Argent. **17**:92. 1884; not *P. rugosa* Billings 1871.

O. Pycnia amphigenous, among the telia, few, gregarious, noticeable, yellowish, subepidermal, globose or somewhat flask-shaped, 125–130 by 125–130 μ, ostiolar filaments not extruded.

III. Telia amphigenous or chiefly epiphyllous and caulicolous, numerous, crowded on yellowish spots in orbicular or somewhat irregular areas, 0.5–5 mm. across, roundish, 0.2–0.5 mm. across, tardily naked, becoming pulverulent, reddish brown, ruptured epidermis conspicuous; teliospores ellipsoid, 18–26 by 30–42 μ, rounded at both ends or occasionally tapering below, not or slightly constricted, cells easily separating; wall cinnamon brown, uniformly thick, 2.5–3 μ or occasionally thickened to 4–5 μ over pores, which are located about half way from apex to septum in the upper cell

and similarly placed between pedicel and septum in the lower cell; noticeably and evenly rugose; pedicel short, colorless, deciduous.

On *Vernonia patens* HBK., Orotina, Costa Rica, January 1, 1916, *Holway* 343; *Vernonia* sp., Colombia, Panama, September 1890, *G. Lagerheim*.

This species is based on specimens collected by *E. Ule* (1686) at Serra Geral, Brazil, February 1891, on an unknown composite. Later DIETEL (Hedwigia **38**:251. 1899) refers a specimen to this species collected by *Ule* (2336) on *V. Tweediana*, at Gavea, Rio de Janeiro, Brazil, June 1897. The first specimen mentioned has not been examined by the writer, but a specimen on *V. Tweediana* from the herbarium of HOLWAY, collected by *Ule* at Jacarepagua, Rio de Janeiro, October 1897, bearing the same number (2336) as the Gavea specimen, has been studied. This material agrees with Sydow Ured. 1605 on the same host from Gavea, Brazil, collected by *Höhnel*, August 1899 and referred to *P. rugosa* Speg. A specimen in the herbarium of the New York Botanical Garden on *Vernonia* sp. from Campinas, Brazil, collected by *F. Noack*, May 1898, is the same. The specimen from Panama is in the herbarium of the New York Botanical Garden and is marked *P. panamensis* Lagerh. n. sp., which was apparently never described. MAYOR (Mem. Soc. Neuch. Sci. Nat. **5**:511, 512. 1913) reports this species as *P. rugosa* Speg., on *V. patens* and *V. scabra*, from Colombia, having made several collections on the former host and one on the latter. None of MAYOR'S collections have been seen, but a specimen was obtained on *V. scabra* in the phanerogamic collection of the Field Museum (sheet 137666) made at Santa Marta, Colombia, December 1898–1901 by *H. H. Smith* (613). The type of *P. rugosa* has not been seen. The description and range indicate, however, that it is identical with *P. rotundata*, as has been previously assumed by SYDOW (Monog. Ured. 1:176. 1902). *P. rugosa* was described as occurring on an unknown composite, questionably *Verbesina*. Its exact status will remain somewhat in doubt until authentic material can be compared.

22. **Puccinia discreta** Jackson and Holway, sp. nov.

O. Pycnia epiphyllous, surrounded by the telia, few, gregarious, noticeable, subepidermal, golden brown fading to dark brown, globoid or depressed globoid, 90–100 by 100–130 μ; ostiolar filaments short.

III. Telia chiefly epiphyllous, densely gregarious and confluent in groups 0.5–3 mm. across, on yellowish hypertrophied spots, often arranged in a concentric manner around the pycnia, roundish or somewhat irregular, 0.2–0.6 mm. across, early naked, at first punctiform, becoming pulverulent, dark cinnamon brown, ruptured epidermis conspicuous; teliospores ellipsoid, 18–22 by 32–42 μ,

rounded at both ends, cells easily separating, strongly constricted at septum, wall dark cinnamon brown, uniform in thickness, 2.5–3.5 μ, minutely verrucose-rugose, often in lines extending in various directions; pore of apical cell placed about half way from apex to septum, similarly in lower cell; pedicel colorless, usually deciduous.

On *Vernonia Deppeana* Less., San Jose, Costa Rica, December 15, 1915, *Holway* 260 (type), January 3, 1916 (363), January 10, 1916 (406), December 27, 1915 (305); Sierra de las Minas, alt. 3500, El Rancho, Dept. Baja Verapaz, Guatemala, January 3, 1908, *W. A. Kellerman* 7026; San Felipe, Retalhuleu, Guatemala, January 14, 1917, O, III, *Holway* 721; Colomba, Dept. Quezaltenango, Guatemala, February 2, 1917, *Holway* (818).

A very distinct species, related to *P. rotundata* Diet., but easily separated by the strongly constricted teliospores and in the less conspicuous character of the markings of the teliospore wall.

23. **Puccinia inaequata** Jackson and Holway, sp. nov.

O. Pycnia epiphyllous, few, gregarious in the center of lighter colored spots, noticeable, subepidermal, depressed globoid, 100–120 μ high by 100–175 μ broad; ostiolar filaments short.

II. Primary uredinia chiefly epiphyllous, crowded and somewhat confluent in concentric groups, 2.2 mm. across, surrounding the pycnia, early naked, pulverulent, cinnamon brown, ruptured epidermis conspicuous; secondary uredinia amphigenous, numerous, scattered, roundish, small, 0.2–0.5 mm. across, early naked, pulverulent, cinnamon brown, ruptured epidermis noticeable; urediniospores obovoid or broadly ellipsoid, 18–23 by 23–28 μ, pale cinnamon brown, 1.5–3 μ thick, prominently and sparsely echinulate, pores 2 or 3, approximately equatorial.

III. Telia amphigenous, scattered, round, small, 0.2–0.5 mm. across, early naked, at first pulvinate becoming somewhat pulverulent, blackish brown, ruptured epidermis conspicuous; teliospores oblong or broadly ellipsoid, 22–26 by 30–38 μ, rounded at both ends, not or scarcely constricted; wall dark cinnamon or chestnut brown, 2.5–3 μ, slightly thickened at apex, 4–5 μ; finely and evenly verrucose-rugose; pedicel colorless, short, usually deciduous, often laterally attached; pore of lower cell below the middle.

On *Vernonia patens* H.B.K., Esquintla, February 17, 1916, *Holway*, O, I, II, 502 (type); Mazatenango, February 22, 1916, II, *Holway* 513; Sanarate,

III, February 10, 1916, *Holway* II, III, 470; Retalhuleu, February 26, 1916, O, II, *Holway* 534; Salama, March 2, 1907, *Kellerman;* El Rancho, January 25, 1905, *Kellerman* 5337; Agua Caliente, February 10, 1917, II, III, *Holway* 851; Santa Rosa, February 1893, *Heyde* and *Lux*, from phanerogamic specimen 4524 Plantae Guatemalensibus, ed. by JOHN DONNELL SMITH, in the Columbia University collection.

This species is known only from the localities listed above in Guatemala. It is easily separated from all other species on *Vernonia*, having distinct rugose markings on the teliospore wall, and by the small spores thickened at the apex.

24. PUCCINIA PINGUIS Diet. Hedwigia **36**:32. February 1897; not *P. pinguis* Diet. and Holw. July 1897.

Known only from the type collection on *Vernonia platensis*, Serra Geral, Brazil, February 1891, *E. Ule* 1692. A part of the type from the herbarium of HOLWAY has been examined, and it proves to be quite distinct. The teliospores are irregularly ellipsoid or oblong, 24–30 by 42–52 μ, slightly or not constricted, wall chestnut brown, 2.5–4 μ thick, apex usually abruptly thickened by a subhyaline papilla to 5–9 μ. Some spores show scarcely any thickening. The wall is obscurely and very minutely rugose. A few colorless urediniospores were observed in one mount. They are globose or broadly ellipsoid, 20–23 by 20–23 μ, wall 1–1.5 μ thick, very minutely and closely echinulate.

25. **Puccinia Kuntzii,** sp. nov.

O and I. Pycnia and aecia unknown.

II. Uredinia not seen; urediniospores intermingled with teliospores, somewhat irregularly globoid to ellipsoid, 26–29 by 29–34 μ; wall golden brown, 3–3.5 μ thick, closely echinulate, pores obscure, probably scattered.

III. Telia hypophyllous, numerous, scattered, roundish, 0.2–0.5 mm. across, early naked, becoming pulverulent, blackish brown, ruptured epidermis not conspicuous; teliospores broadly ellipsoid or oblong, rounded at either end, occasionally somewhat narrowed below, not or slightly constricted, wall dark chestnut brown, 5.5–7.5 μ thick, apex slightly thickened 8–10 μ, prominently and closely verrucose-rugose, pore of lower cell situated midway between septum and pedicel; pedicel colorless, flexuous, one half to twice length of spore, often deciduous.

The specimen on which this species is based was obtained from a phanerogamic specimen in the herbarium of the New York Botanical Garden, labeled

Vernonia Kuntzii Hieron., Santa Cruz, Bolivia, May 1892, *Otto Kuntze*. It is perhaps related to *P. semiinsculpta*, from which it differs chiefly in the broader, more closely echinulate urediniospores.

26. PUCCINIA PAUPERCULA Arth. BOT. GAZ. **40**:206. 1905.—*P. Elephantopodis-spicati* Pat. Bull. Soc. Myc. Fr. **28**:140. 1912.

This species, known only on *Elephantopus spicatus* Juss., was originally described from a collection made by *E. W. D. Holway* (3074) at Vera Cruz, Mexico, October 5, 1898. A second collection was made by *Holway* at San Jose, Costa Rica, January 3, 1916 (353). Collections have also been made by *Holway* at Mazatenango, Guatemala, February 21, 1916 (510A); February 25, 1916 (530).

It is a lepto-form with telia in orbicular groups 1–4 mm. across. The spores are oblong or lanceolate oblong, 15–17 by 39–50 μ, acute or obtuse at apex, obtuse or narrowed at base, and scarcely constricted at the septum. The wall is smooth, chestnut brown, rather thin, 1–2 μ and considerably thickened to 7–9 μ at apex. The pedicel is firm, colored like the spore, about one-half the spore length.

The type of *P. Elephantopodis-spicati* Pat. was described from material collected by *Tonduz* at San Francisco de Guadalupe, Costa Rica, July 1908. A portion of the type has been examined and agrees in all essential features with the type of *P. paupercula* and occurs on the same host species.

27. PUCCINIA ELEPHANTOPODIS P. Henn. Hedwigia Beibl. **39**:154. 1900.

This species, known only from the type collection made at Santa Anna, Argentina, by *G. Neiderlein*, January 22, 1883, on *Elephantopus angustifolius*, is interpreted by SYDOW as being a micro-form. He states that the urediniospores described by HENNINGS are single cells of the teliospores. The latter are described as ovoid, subcuneate to ellipsoid, 18–23 by 25–33 μ, wall minutely verrucose, 3–4 μ thick, light brown, apex not or scarcely thickened, constricted at the septum, pedicel hyaline, short, fragile. This species has not been seen by the writer, and the assignment in the preceding key is largely based on SYDOW's interpretation.

28. PUCCINIA PIPTOCARPHAE P. Henn. Hedwigia **35**:240. 1896.

This species was described from two specimens collected at St. Catharina, pr. Blumenau, Brazil, by *E. Ule*, one on *Piptocarpha oblonga*, the other on *Piptocarpha* sp., December 1888, nos. 1317, 1198. Specimens of both collections have been examined by the writer. The urediniospores are globoid, 27–32 by 29–34 μ, wall cinnamon brown, 1.5–2.5 μ in thickness, moderately and strongly echinulate, the pores obscure but apparently 4–6, scattered. The teliospores are oblong clavate or ellipsoid, 26–29 by 45–56 μ, apex and base rounded, somewhat constricted, wall cinnamon brown, 1 μ or less in thickness, smooth, wall slightly thickened to 2.5 μ at apex.

29. PUCCINIA LEPTODERMA Diet. Hedwigia **38**:251. 1899.

While evidently related to the preceding species, the form differs markedly in the width of the teliospores, which are described as ellipsoid to oblong, 28–35 by 45–60 μ, constricted at septum, but not thickened at apex. No uredinia or urediniospores are described. This species has not been seen by the writer. It was reported on *Piptocarpha* sp. from Maná, Rio de Janeiro, Brazil, August 1896, *E. Ule* (2334).

EXCLUDED SPECIES

PUCCINIA VERNONIAE Cke. Grevillea **10**:26. 1882.

This species has not been seen. It was based on several collections made in Natal by *Wood*. The teliospores are evidently immature, as stated by COOKE in the original description and reaffirmed by SYDOW (Monographia Uredinearum 1:178. 1902), who has apparently examined an original specimen. In any case the name is untenable (cf. 13). It seems best, therefore, to disregard this species in the present account.

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PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION
LA FAYETTE, IND.

THE RAY SYSTEM OF QUERCUS ALBA

LaDema M. Langdon

(WITH TWENTY-TWO FIGURES)

Introduction

The medullary rays of *Quercus alba* are of three distinct types: uniseriate rays, thin, linear sheets of tissue of a single layer of cells; multiseriate rays, two or more cells in width and many cells in height; and compound rays, which are broader than either of the first two mentioned and consist of extensive homogeneous masses of parenchyma. Between the uniseriate and the compound types there exist numerous transitional stages, representing either disintegration of the broad ray into a number of narrow ones or the integration of many uniseriate rays to form the compound rays. Figs. 9 and 10 illustrate these three principal types.

The evolution of these different types of rays and the relationships between them have recently been the cause of much discussion and the subject of a series of investigations carried on chiefly in the laboratories of Harvard University. This particular line of investigation was initiated in 1909 by Jeffrey (7) when he proposed the "aggregate ray hypothesis." He maintains that paleobotanical evidence points to the probable derivation of the existing oaks from ancestors which possessed only the linear type of ray, and that the broad rays so characteristic of the present oak wood have been formed by a gradual aggregation of uniseriate rays. His arguments favoring the "aggregate ray hypothesis" have since been perfected and worked out in greater detail by Eames (5, 6) and by Bailey (1, 2, 3). Eames (5) has demonstrated from a study of fossil and seedling oaks that the broad type of ray has originated by the aggregation or fusion of many of the small uniseriate rays through the transformation of the included fibers and wood parenchyma into ray parenchyma. He agrees with Jeffrey (7) that in the fossil oaks and in the seedlings of modern oaks only the linear type of ray is found. Bailey (2) has developed

this particular theory and asserts that the great factor at work in the formation of the compound ray is the influence of the leaf trace. Since the stem adjacent to the leaf trace is the most natural storage place for food manufactured in the leaf, he concludes that the storage organs, the rays, would be enormously developed at this particular point in the stem for the purpose of storing assimilates descending from the large persistent leaves of Mesozoic angiosperms. Following its formation at the leaf trace, the broad ray has spread throughout the tree. These "foliar" rays, as BAILEY calls them, have persisted in the families of the dicotyledons either in their very primitive "aggregate" condition (composed of congeries of small rays) or in their more advanced "compound" condition (completely parenchymatous).

A second line of evidence which amplifies this original hypothesis is advanced by THOMPSON (8). He maintains that the "multiseriate" type of ray has originated from the diffused portions of "aggregate" or "compound" rays. With the advent of a severe winter season and the consequent acquirement of the deciduous habit by the leaves, the organization of storage systems about the leaf trace was no longer of advantage. Thus in the development of the multiseriate ray, which characterizes the majority of living dicotyledons, portions of the aggregate or compound rays have been diffused more or less uniformly throughout the stem.

In opposition to the aggregate ray hypothesis, BAILEY and SINNOTT (4) in a more recent article suggest the possibility that the clusters of small rays may be, in many cases, stages in the breaking down rather than the building up of wide rays. They state that the multiseriate ray has originated merely by the gradual increase in width of the primitive uniseriate ray, and that in all probability the so-called "aggregate" rays, instead of being formed by the fusion of many smaller linear rays, are merely stages in the reduction and disintegration of the wide multiseriate rays.

Material and methods

About January 1, 1916, specimens of white oak twigs varying in age from 1 to 19 years were collected from three different trees on the campus of Oberlin College and from three different regions

of each of these trees. Likewise, from each tree twigs of unusual vigor of growth and shoots suppressed in their growth were procured. For convenience the trees were numbered I, II, and III. Trees I and III are of about the same age, 55–60 years old, but tree I is larger and of slightly more vigorous growth than III. Tree II is younger than either I or III, about 35–40 years old.

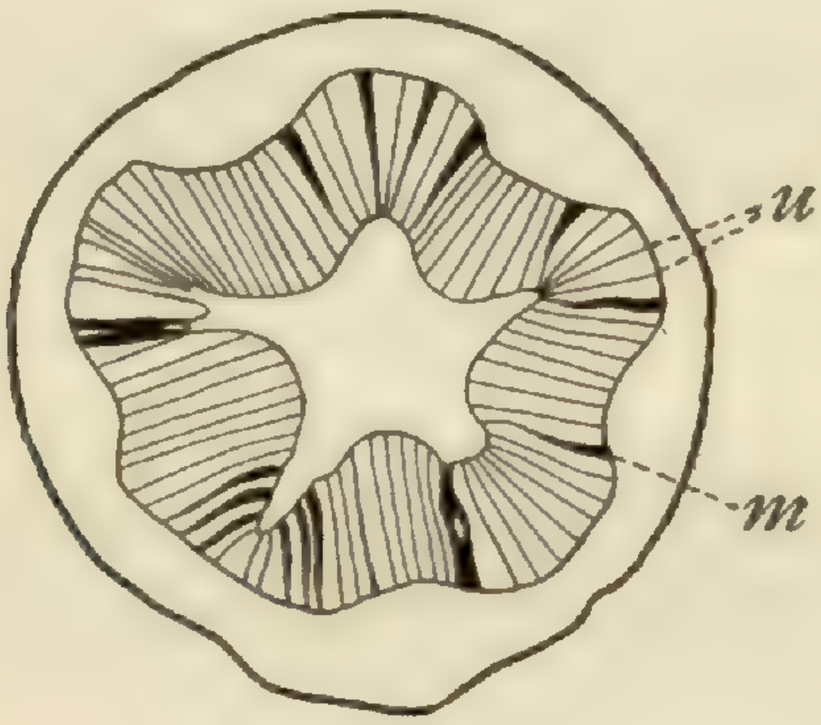
In the preparation of the wood for sectioning the process taken from CHAMBERLAIN'S *Methods in Plant Histology* was followed with slight modifications. The specimens of wood gathered from the different regions of these three trees were cut into small blocks and treated with hydrofluoric acid. After treating with the acid, wood should be left in equal parts glycerine and 30 per cent alcohol for several days or even weeks before sectioning to prevent the cortex of the stem from separating from the xylem.

A series of transverse and tangential sections, both nodal and internodal, was made of twigs of all ages from 1 to 19 years, taken from the lower, center, and top portions of all three trees. This afforded an opportunity to compare woods of the same age and vigor of growth from different parts of the same tree and also from different trees, thus to ascertain whether certain ecological conditions, such as age of trees and vigorous or suppressed conditions of growth, may not tend toward the modification of the ray system of *Quercus*.

Observations

THE FIRST ANNUAL RING.—Although the uniseriate ray is the predominating type in the first formed secondary xylem of *Quercus alba*, multiseriate rays 2–6 cells in width also occur, radiating in pairs from the 5 lobes of the pith (fig. 1). Since these lobes or deep extensions of the pith into the surrounding woody tissue mark the region of leaf gaps, the initiation of pairs of wide rays at these particular points clearly indicates the relation of these rays to the two lateral leaf traces passing out at alternating nodes. Both the wide and the linear rays extend radially from the pith through the phloem to the band of sclerenchyma separating the phloem and cortex regions of the stem. The effect of vigorous growth upon the general structure of the stem, and especially upon the ray system, is particularly noticeable in the first annual ring. Not only are

the multiseriate rays more numerous and parenchymatous, but the ring of growth is wider and the vessels and tracheids correspondingly larger in the vigorous (figs. 1, 2, 3, 4) than in the non-vigorous or suppressed year old twigs (figs. 7, 8).



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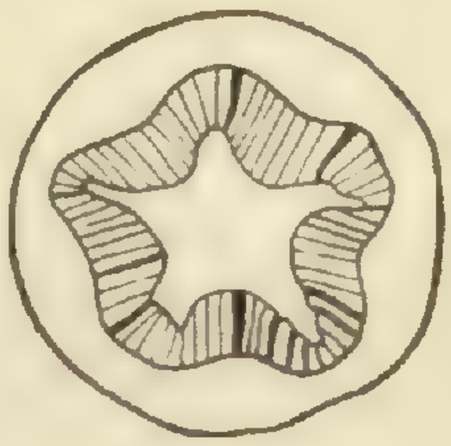

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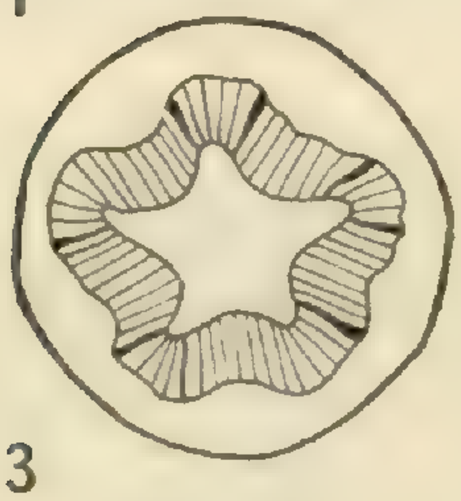

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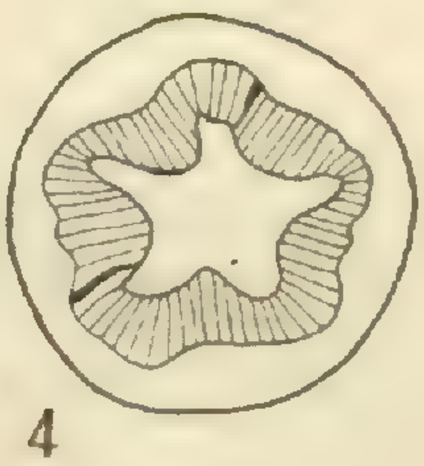

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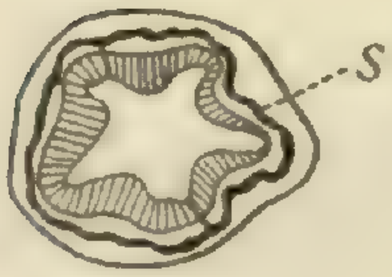

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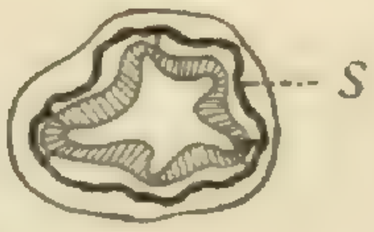

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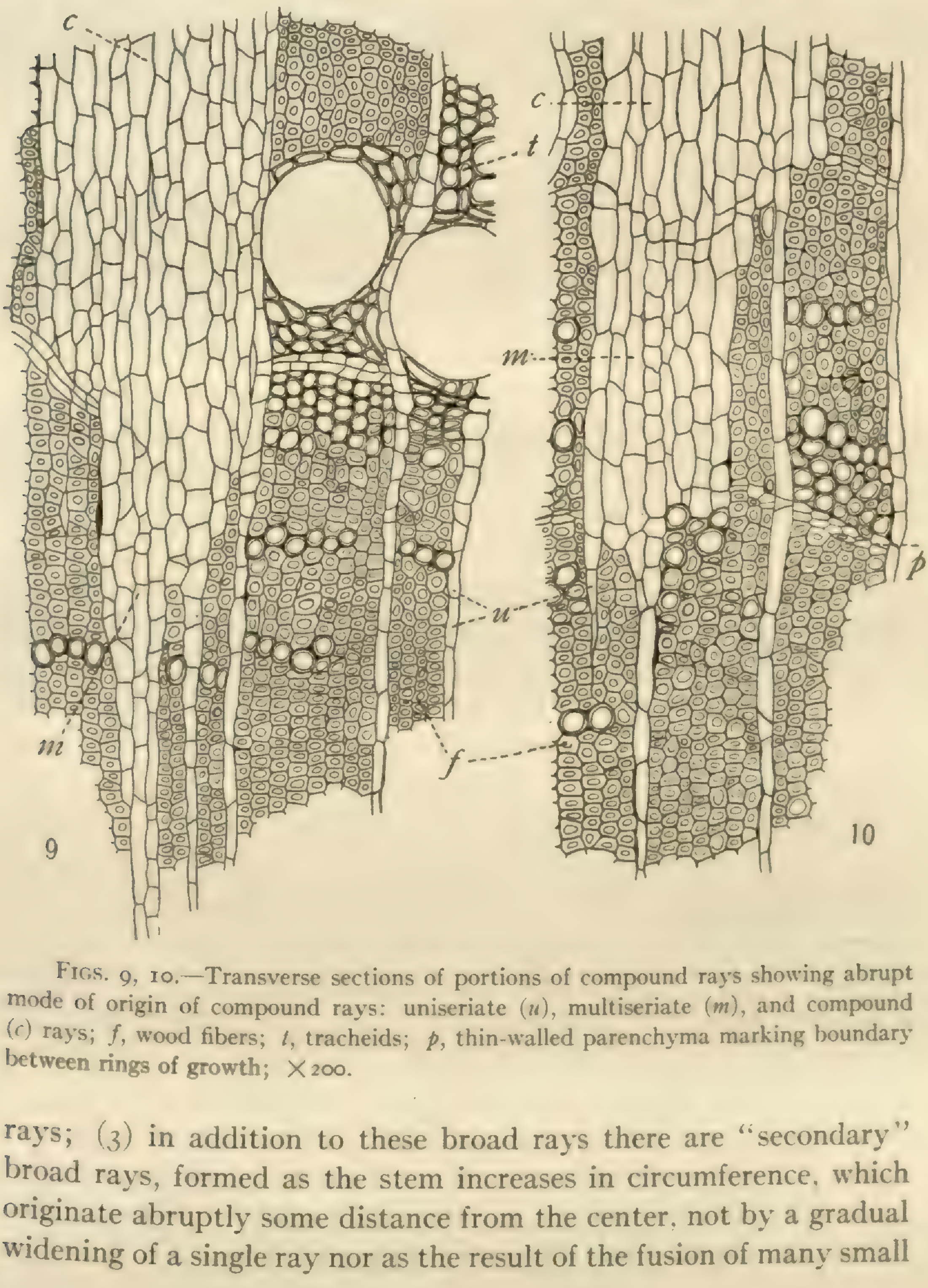
FIGS. 1–8.—Transverse sections of year old twigs: fig. 1, section cut just above node, of unusually vigorous year old shoot from upper part of tree I; *u*, uniseriate rays, *m*, multiserate rays; figs. 2–4, sections cut just below node, from lower (2), center (4), and top (3) regions of tree I; figs. 5, 6, sections cut slightly below node of twigs from top (5) and lower part (6) of tree III; *s*, wide bands of sclerenchyma; figs. 7, 8, sections of suppressed year old shoots from top (7) and lower regions (8) of tree II; ×5.5.

SHOOTS FIVE TO NINETEEN YEARS OLD.—In general the three types of medullary rays previously described as characteristic of the white oak wood occur in all shoots from 5 to 20 years old, but there are three distinct types of compound rays: (1) rays which

are broad, high, gradually tapering wedges, usually formed by the gradual widening of a single uniseriate or triseriate ray which has its origin at the pith; (2) compound rays, which are wide sheets of ray parenchyma formed by the aggregation of many small linear



FIGS. 9, 10.—Transverse sections of portions of compound rays showing abrupt mode of origin of compound rays: uniseriate (*u*), multiseriate (*m*), and compound (*c*) rays; *f*, wood fibers; *t*, tracheids; *p*, thin-walled parenchyma marking boundary between rings of growth; ×200.

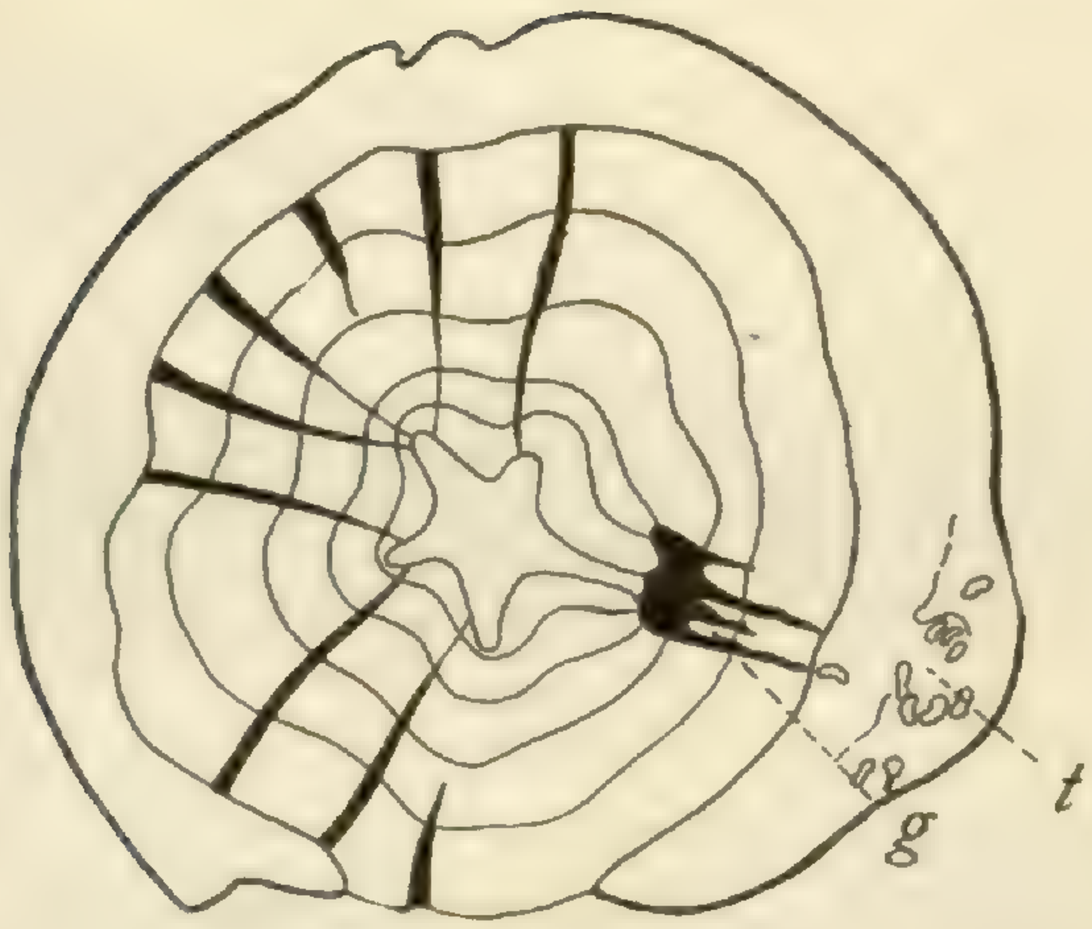
rays; (3) in addition to these broad rays there are "secondary" broad rays, formed as the stem increases in circumference, which originate abruptly some distance from the center, not by a gradual widening of a single ray nor as the result of the fusion of many small

rays, but by a sudden checking of the development of all tracheidal tissue within the immediate vicinity of the ray and the consequent continued growth of parenchyma in this region. This abrupt change usually occurs at the beginning of a year's growth. Figs. 9 and 10 show transverse sections of portions of such rays at the points where they abruptly broaden, and illustrate very clearly the manner in which this type of ray originates. These three types of compound rays occur generally in all sections of the mature wood, but the wedge-shaped, gradually tapering ray, as seen in transverse section, appears to be the characteristic type of broad ray in this species of oak.

A very peculiar and constant feature of the multiseriate and compound rays is the manner in which they are broken up, upon entering the cortical region of the stem, into wedge-shaped masses of ray parenchyma. No such interruption or breaking up of the thin, linear uniseriate rays is apparent.

A careful study of different sections from the lower, central, and top regions of the same tree (figs. 11, 12, 13) makes it evident that the region of the tree from which the wood comes is only a slight factor, if any, in the modification of the ray system. On the other hand, a comparison of all sections of shoots of the same age from the three trees reveals a marked diminution in the diameters of stems from trees II and III, but this may be due chiefly to the effects of retardation in growth of these two trees rather than to a difference in age.

EFFECT OF SUPPRESSED GROWTH ON RAY SYSTEM.—The retarding effect of suppressed growth on the medullary ray development is easily seen in figs. 17, 18, and 19. Although wide rays occur in these suppressed twigs, they are neither so wide nor so deep as in the case of the vigorous shoots. Especially in some of the older stems from tree III the development of wide rays has been retarded to such an extent that only uniseriate rays occur, even in mature 11 and 12 year old wood (fig. 22); and in numerous specimens of wood 15–19 years old, taken from different regions of this same tree, wide rays are entirely absent up to about the tenth or eleventh year, when broad rays often appear abruptly, the phase of compounding being confined to one or two annual rings (fig. 16).



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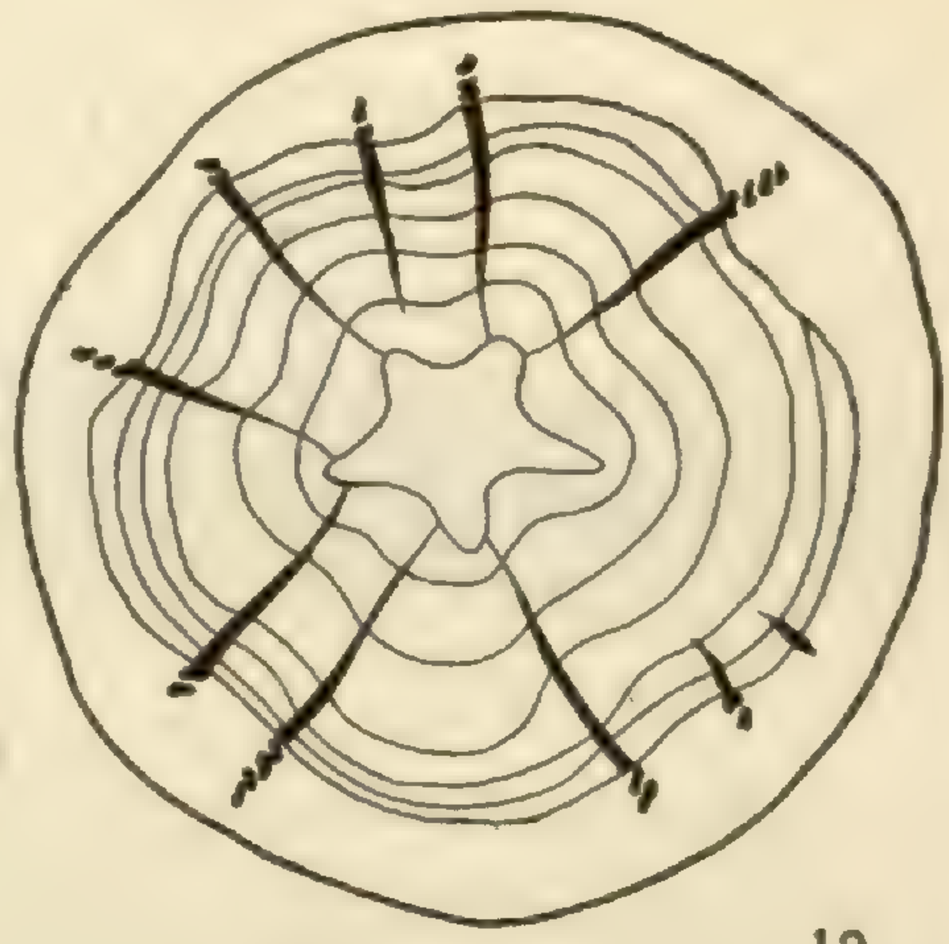

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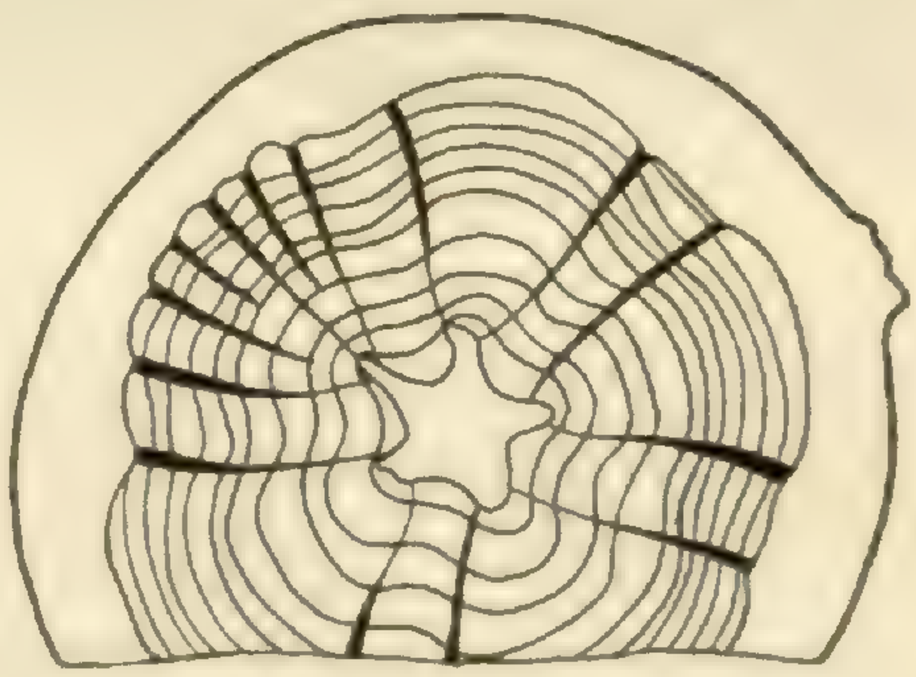

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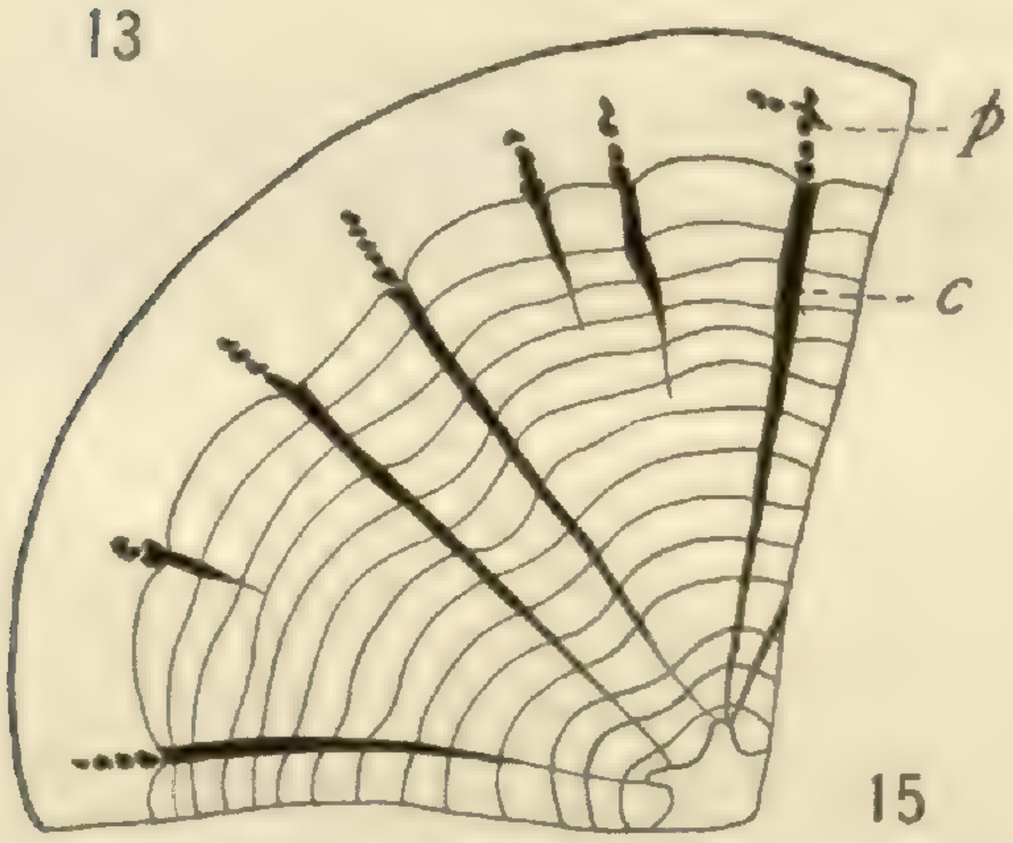

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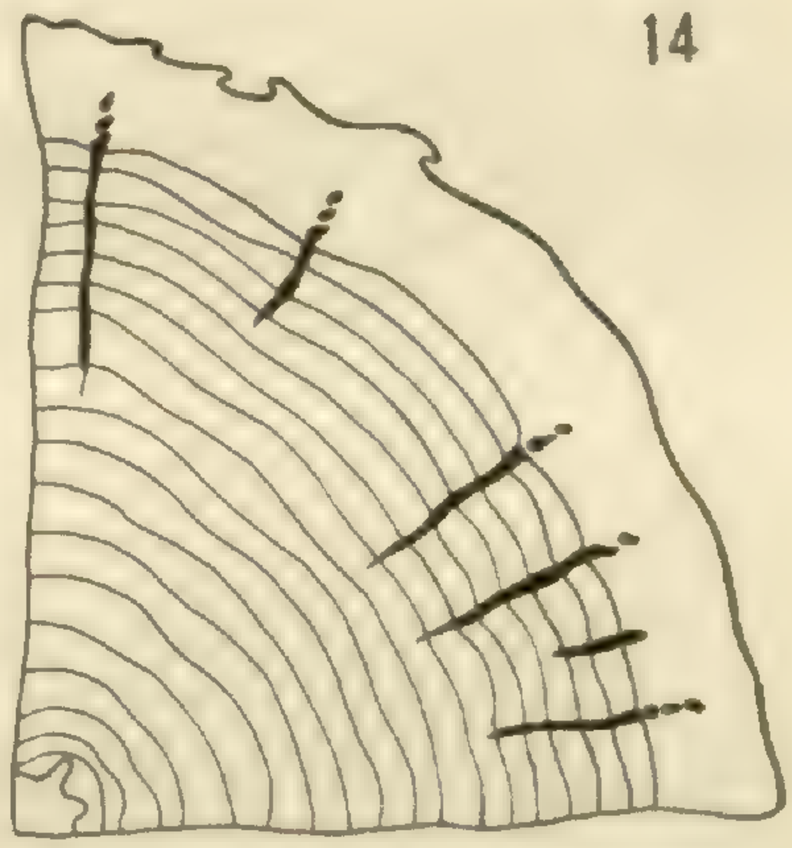

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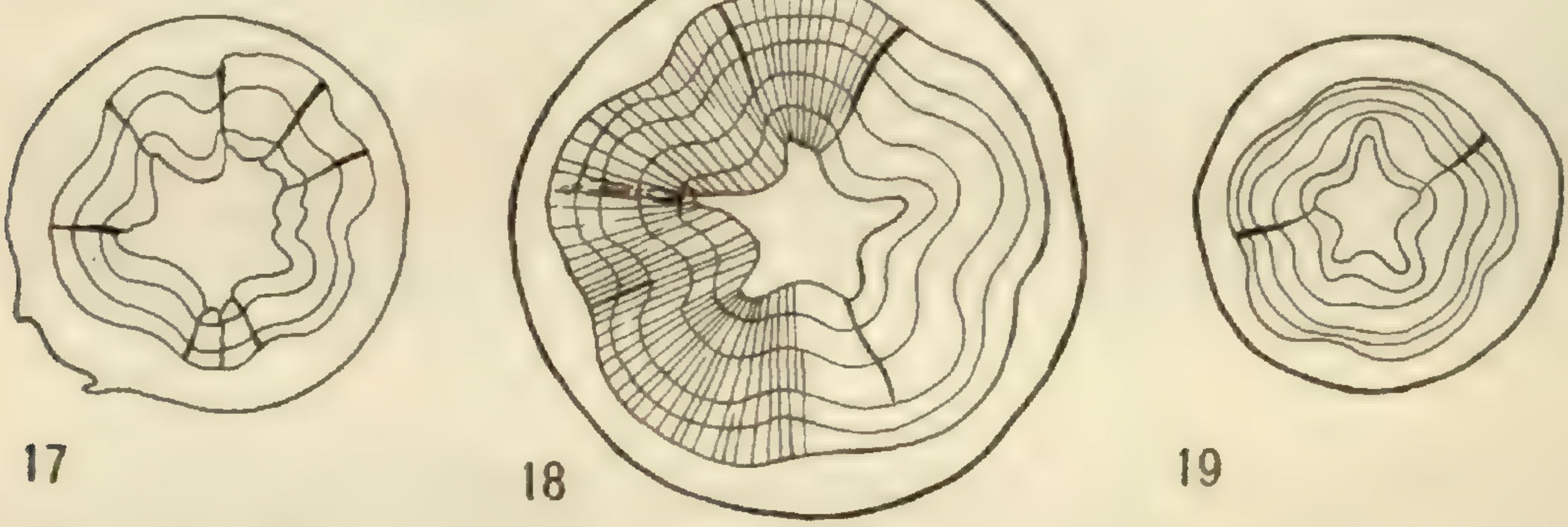
FIGS. 11–16.—Transverse sections: fig. 11, nodal section of 5 year old twig from lower part of tree I, showing well developed broad rays; *g*, leaf gap; *t*, leaf trace; figs. 12, 13, internodal sections of shoots from central (12) and top (13) regions of tree I; *c*, compound rays; fig. 14, section of 10 year old wood from tree III; fig. 15, section of vigorous 14 year old branch from central region of tree I; broad rays broken upon entering cortical region into wedge-shaped masses of ray parenchyma (*p*); fig. 16, section of suppressed 19 year old branch from tree III; figs. 11–14, ×5.5; figs. 15, 16, ×4⅛.

Discussion

Another notable feature of the wood of *Quercus alba* is its conspicuously ridged and depressed outline. Cross-sections of the twigs show 5 protruding wedge-shaped segments of secondary xylem which include between them 5 narrow, depressed segments, separated from the protruding ones by the great lateral leaf trace rays. This peculiar formation is especially noticeable in the stems



FIGS. 17–22.—Figs. 17–19, transverse internodal sections of 3 and 5 year old twigs from lower branches of tree III, showing retarded development of multiseriate rays; fig. 20, internodal section of 5 year old twig from top branch of tree II; fig. 21, section, cut near node, of 5 year old stem from upper branch tree III; fig. 22, section of suppressed 12 year shoot from central region of tree III; striking illustration of effect of suppressed growth upon medullary ray development; ×5.5.

of shoots 1–10 years old and gradually becomes less prominent in the older woods. BAILEY (**2**) accounts for this peculiarity of the oak wood on the ground that the medullary rays or storage tissue associated with the lateral leaf traces have a strong retarding influence on the surrounding tissue, thus accounting for the marked difference between the general rate of growth of the woody tissue

and that of the large aggregate rays. When the rays are strongly developed, the dipping in of the annual ring where it crosses a large ray is sharper, thus explaining the narrow, depressed segments.

From observations of transverse sections of twigs from *Quercus alba*, *Q. bicolor*, and *Q. macrocarpa* I find that there is evidence of retardation in growth of the tissues in the immediate vicinity of the wide rays, especially noticeable in the marked dipping in of the annual rings where they cross the large rays. However, aside from a few extreme cases, this checking influence of the wide foliar rays does not explain the 5 conspicuous depressions so characteristic of the wood of *Quercus*. Their cause may be traced more directly to the effect of the leaf traces upon the general growth and form of the woody cylinder. Since the principal function of the xylem is the conduction of water from the soil to the outer parts of the plant, it is obvious that the maximum upward movement of solutions in the stem would be through the tracheidal tissues and vessels in direct line with the leaf traces. This would cause an acceleration in growth and the consequent outward projection of those 5 regions of the woody cylinder associated with leaf traces, while the neighboring conducting tissues, namely, the so-called depressions from which the main conducting streams had been diverted to the petioles of the leaves, would fail to maintain their normal rate of growth.

This condition of the secondary xylem may persist for a number of years, but there is a gradual diminution in the size of the depressions until at length the cambium layer and the xylem assume a circular outline. This may be due to the fact that as the wood increases in age its capacity for water conduction decreases, owing to the choking of the lumina of the vessels of the central regions of the wood with tyloses. In typical heart wood trees, such as the oak, the sap wood is limited in certain species to the youngest annual ring, and in some cases merely to the tracheary tissues of this ring. The narrowing of the active conducting zone would then be likely to cause a more even development of the woody tissues around the entire stem. A fact worthy of note in connection with this characteristic formation of the cambium and xylem in the stem of the oak is that corresponding to the degree of

depression of the secondary xylem in the concave segments is the proportionate increase in amount of phloem above these segments.

With two exceptions, all of the seedlings used in this investigation were germinated and grown under greenhouse conditions, averaging 1.75–3 inches in height. Here, as in the case of the first annual ring, uniseriate rays are the prevailing type, multiseriate rays 3 and 4 cells in width appearing only in the vicinity of lateral leaf traces.

Summary

1. It was chiefly with the purpose of determining the effect of certain conditions upon the ray system of *Quercus alba*, such as the age of the trees, location of shoots in the trees, and vigorous or suppressed conditions of growth, that this investigation was undertaken.

2. The results obtained indicate that neither the age of the trees nor the location of wood in a tree is an appreciable factor in the modification of the ray system.

3. The conditions of vigorous and suppressed growth, however, are problems to be considered. With decreasing vigor of growth in the mature wood multiseriate rays appear at progressively later stages in the development of the stem.

4. Multiseriate rays, 2–6 cells in width, occur in the seedlings and the first annual ring of *Quercus alba* only in the vicinity of lateral leaf traces.

5. The peculiar formation of the cambium and wood in the stem of the oak, whereby 5 wedge-shaped segments of secondary xylem are formed, including between them 5 narrow depressed segments, is due directly to the influence of the outgoing leaf traces upon the general growth and form of the woody cylinder.

This investigation was undertaken at the Botanical Laboratory of Oberlin College, and the sincerest thanks of the writer are due to Professor FREDERICK O. GROVER and to Dr. SUSAN P. NICHOLS for their kind assistance. Grateful acknowledgment is also made of the valuable criticism and advice given by Dr. CHARLES J. CHAMBERLAIN and Dr. W. J. G. LAND during the continuation of the work at the University of Chicago.

UNIVERSITY OF CHICAGO

LITERATURE CITED

1. BAILEY, I. W., Reversionary characters of traumatic oak wood. BOT. GAZ. **50**:374–380. 1910.
2. ———, The relation of the leaf trace to the formation of compound rays in the lower dicotyledons. Ann. Botany **25**:225–241. 1911.
3. ———, The evolutionary history of the foliar ray in the wood of the dicots, and its phylogenetic significance. Ann. Botany **26**:647–661. 1912.
4. BAILEY, I. W., and SINNOTT, E. W., Phylogeny of the angiosperms. BOT. GAZ. **58**:36–58. 1914.
5. EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. **49**:161–166. 1910.
6. ———, On the origin of the herbaceous habit in angiosperms. Ann. Botany **25**:215–224. 1911.
7. JEFFREY, E. C., The progress of plant anatomy during the last decade. Amer. Nat. **43**:230–237. 1909.
8. THOMPSON, W. P., On the origin of the multiseriate ray of the dicotyledons. Ann. Botany **25**:1005–1014. 1911.

BEARING OF HETEROSIS UPON DOUBLE FERTILIZATION

DONALD F. JONES

(WITH THREE FIGURES)

The increase in development frequently observed in generations immediately following a cross in both plants and animals has been definitely correlated with heterogeneity of germinal constituents. The diverse effects resulting from this heterozygous condition have all been included in the one term heterosis (14). Various ways in which heterosis in plants may become visible have been described by different investigators. An increase in general vegetative luxuriance was first recorded by KÖLREUTER (11) as early as 1766. An increase in the facility of vegetative propagation has been shown for hybrids as well as an increased viability under adverse climatic conditions (GÄRTNER 9, and references given there). DARWIN (7) gives numerous cases in which the rate of growth was increased by crossing. Both the time of flowering and maturing was hastened, as compared with the parents, in a large number of crosses, which also gave an increase in size.

To these many manifestations of the effects of heterozygosis COLLINS and KEMPTON (2) have added the fact that in maize the endosperm may also be increased in amount as an immediate result of crossing. By artificially pollinating maize with a mixture of two kinds of pollen, two visibly different kinds of seed were obtained upon the same ear (pistillate inflorescence) by taking advantage of xenia. The varieties of maize used in making these crosses differed among other characters in the color of the aleurone cells of the endosperm. A mixture of pollen of a variety with uncolored aleurone and of pollen of a variety with colored aleurone, when applied to the ear of a plant with uncolored aleurone, gave colored and uncolored seeds. In this way 11 ears were obtained, with the two kinds of seeds distributed at random. To produce the uncolored

seeds, pollen from the same plant or another plant of the same variety was used. These seeds were then either selfed, or crossed with a closely related plant. The colored seeds, however, were the result of a cross with a different variety. The two kinds of seeds were separated and weighed. It was found that in all the 11 cases the out-crossed seeds exceeded the others in weight by percentages ranging from 3 to 21. Since the two genetically different kinds of seeds developed side by side in the same inflorescence, under as nearly the same conditions as it was possible to obtain, such increases in weight are surely significant.

That the increase in weight was a manifestation of heterosis and not merely the result of crossing a large seeded plant on a small seeded plant, was shown by the fact that where two varieties were used as pollen parents which differed in size of seed, one having seeds twice as large as the other, the crosses involving the large seeded plant showed no greater increases than the crosses in which the small seeded plant was used as pollen parent. In fact, the latter crosses gave rather greater increases. From this COLLINS and KEMPTON conclude that "the rate of increase bears no direct relation to the size of seed in the variety used as the source of pollen" (*loc. cit.* p. 11).

In the experiments of COLLINS and KEMPTON, reciprocal crosses were not made. Although the fact of increased endosperm development resulting from cross-fertilization is shown by the results reported, still more conclusive evidence has been obtained by the writer from reciprocal crosses in maize by the use of similar pollen mixtures. A number of crosses were made between types of maize previously selfed from 3 to 6 generations. These inbred strains were quite uniform and were derived originally from different cultivated varieties. Reciprocal crosses were made, not between individual plants, but between the different strains. All of the plants of each line, however, were descended from individual plants in the preceding generation and were genetically nearly identical.

Some of the strains had yellow, others white endosperm. Either way the cross was made the heterozygous seeds immediately resulting from pollination were light yellow, with a more or less

distinct white or pale yellow cap. The pure yellow seeds in most cases could easily be distinguished from these heterozygous yellow seeds by their darker color and absence of the light colored cap. Mixtures of "white" and "yellow" pollen, therefore, applied either to a white or a yellow seeded plant, produced two distinct classes of seeds which could easily be separated. Some yellow strains were found which, when crossed by white, did not give heterozygous seeds clearly distinguishable from pure yellow. No such crosses were used in comparing the weights of selfed and crossed seeds. The reciprocal cross of yellow on white always gave yellow seeds clearly distinct from pure white, as would be expected.

FIG. 1.—Two ears of maize with uncolored endosperm pollinated with mixture of "yellow" and "white" pollen, showing distribution of selfed and crossed seeds.

In all the ears resulting from the application of mixed pollen, the selfed and crossed seeds were distributed at random (fig. 1). Approximately equal quantities of pollen were used for each pollination, but, owing probably to the short viability of maize pollen (1), the two kinds were not always equal in their ability to fertilize. The proportion of selfed and crossed seeds, therefore, varied greatly. In some cases all the seeds were crossed, in others all selfed.

Twenty-four ears having both selfed and crossed seeds were obtained, and all gave an increase in average weight of the crossed seeds over the average weight of the selfed seeds, ranging from 5 to 35 per cent. The complete data will be published elsewhere, as these results were obtained in connection with a different investigation. A typical distribution of the weights of the selfed

and crossed seeds in a reciprocal combination on two ears is shown in table I.[1]

TABLE I

DISTRIBUTION OF WEIGHTS OF SELFED AND CROSSED SEEDS OF MAIZE GROWN IN SAME INFLORESCENCES

Plant number; seeds grown in same inflorescence	Color of seeds	Condition of seeds	Weight of seeds in centigrams									Total number	Average weight	Increase	Percentage increase
			10	14	18	22	26	30	34	38	42				
14–10–4–6–4–7–26..	Yellow	Selfed				1	7	**53**	11	1		73	30.2±0.19		
14–10–4–6–4–7–26×20A–4–25 37.....	Light yellow	Crossed			1	0	3	12	72	**90**	10	188	35.9±0.16	5.7±0.25	18.9
20A–4–25–36.....	White	Selfed	1	1	2	**63**	2					69	21.7±0.16		
20A–4–25–36×14–10–4–6–4–7–6....	Light yellow	Crossed				6	**33**	5				44	25.9±0.20	4.2±0.26	19.4

The crossed and selfed seeds on one of the ears shown in the table differ by 5.7 cgm. in average weight, a divergence which is 22 times the probable error. The reciprocally crossed ear produced seeds which differ by 4.2 cgm., or 16 times the probable error.

One ear with 5 crossed seeds and 328 selfed seeds gave the largest increase obtained in all the pollinations. The selfed seeds altogether averaged 37.3 cgm. in weight, while the 5 crossed seeds averaged 58.0 cgm. This is an increase of 55 per cent. Among the selfed seeds, however, were all the tip seeds, which were smaller in this ear (as is nearly always the case in maize) than the other seeds. The comparison is therefore unfair to the selfed seeds. Taking only the 10 seeds immediately adjacent to the 5 crossed seeds on the basal and apical sides the increase was still the largest obtained, 35 per cent. The crossed seeds were visibly larger, as shown in fig. 3.

The fact that the greatest increase was obtained where the proportion of crossed to selfed seeds was least, suggested that the heterotic seeds developed at the expense of the selfed seeds. An examination of all the data, however, showed that there was no significant correlation between the amount of increase and the

[1] A Jolly balance was fitted with scale and pointer so that the weights could be read off directly. A pan was constructed out of stiff paper in such a way that pressing the two ends together allowed the seeds to fall out through a slit in the bottom after weighing. This proved to be a great time saver. A magnifying glass helped in reading the scale (fig. 2).

proportion of the two kinds of seeds. Nearly as large increases were obtained where the number of crossed seeds greatly exceeded the selfed. These data obtained from reciprocal crosses fully substantiate the results reported by COLLINS and KEMPTON, and altogether show that CORRENS (5) was not wholly correct in stating that crossing does not immediately alter the size of seeds in maize.

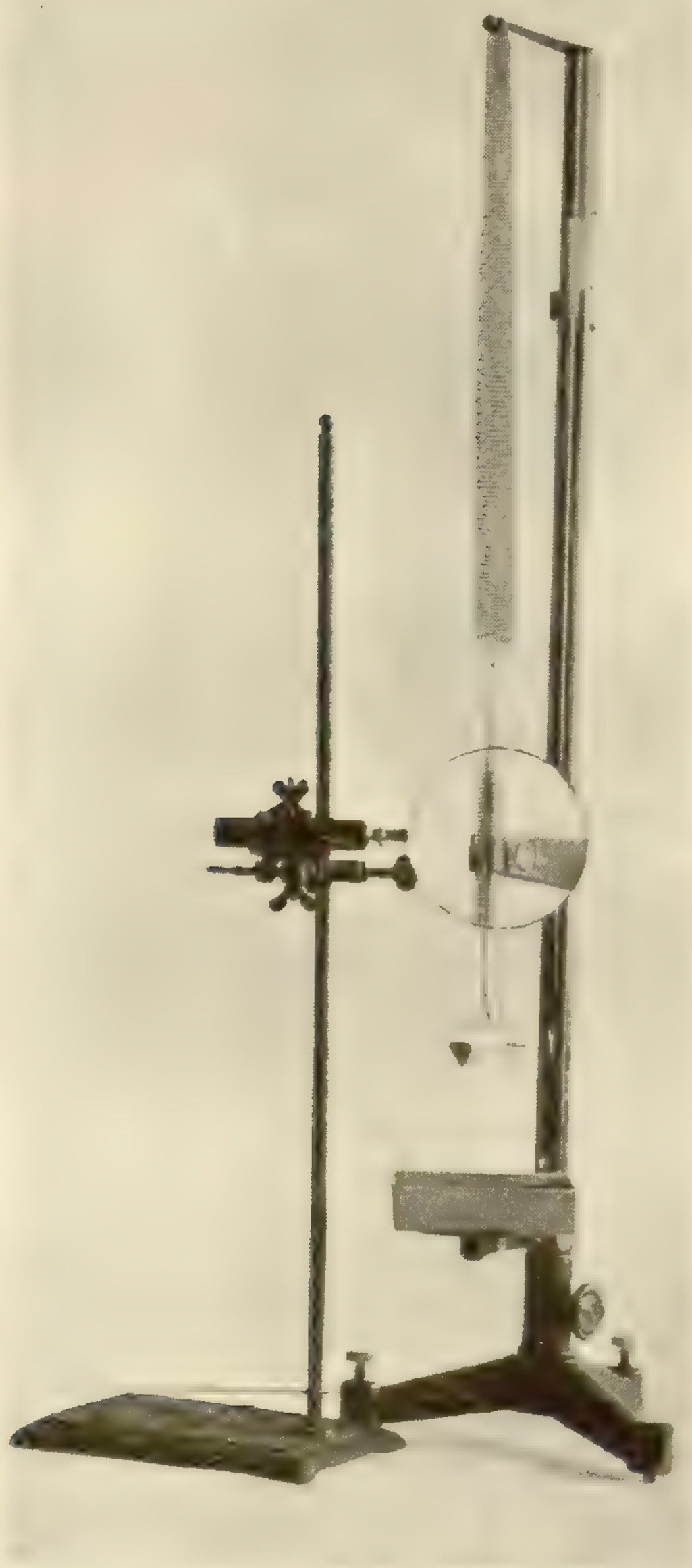


FIG. 2.—Machine used for weighing seeds.

So far as I know, maize is the only plant in which this manifestation of heterosis has been demonstrated. Since the main facts of xenia and heterosis as determined in maize do not differ essentially from the results obtained in other plants, there is every reason to suppose that increased endosperm development resulting from crossing is a phenomenon which may occur in many, if not all, other angiosperms where double fertilization takes place. Granted that this is so, what bearing do these facts have upon the puzzling problem of double fertilization in endosperm formation?

NĚMEC (13) has suggested, as a means of accounting for the origin of the process of endosperm hybridization, that it is an adaptation resulting in an alteration of the food supply to accord with the properties of a hybrid embryo. His own statements in regard to the matter are as follows:

> In a case of hybridization, the embryo and the endosperm are assured the same physiological properties only when the endosperm fusion nucleus as well

as the egg cell are fertilized by nuclei of the same properties, and this takes place in double fertilization. Double fertilization occurs even when the reserve substances entirely or to a great extent are put directly into the embryo, and we see that this is truly the case in many plants. In these plants nevertheless an endosperm at first develops and even results from double fertilization as

FIG. 3.—Crossed and selfed seeds from same inflorescence; top and side view of same seeds; crossed seeds above, selfed seeds below.

well, so it is possible that such plants exhibit a retention of a character and that in them the fertilization of the endosperms is only a useless relic. So from our standpoint double fertilization can be taken as an apparent adaptation in two ways: first, to stimulate endosperm development; second, to alter the endosperm physiologically to accord as far as is possible with the embryo. In this way a good nourishment of the seedlings by the endosperm material is assured (*loc. cit.* pp. 502, 503).

This is indeed an ingenious interpretation. Without endosperm hybridization an embryo resulting from a cross would be forced to depend entirely upon the kind of food supplied by one parent in its early stages of development, as is the case in all plants where double fertilization does not occur. It is conceivable that a wide cross might so alter the developing zygote that it would be less favorably nourished by food furnished by only one parent in the critical stages of its development. Hybridization of the endosperm, no doubt, may help to adapt the food to the requirements of the hybrid embryo more or less intermediate between the two parents. It would be still more serviceable in the rare cases of supposed merogony (**3, 4, 8, 12**). In these cases, however, nothing is known about the development of the endosperm, but what would be the nature of an embryo derived from such a wide cross that it would be retarded in its development because of an ill-adjusted food supply coming from one parent? Such an embryo would be so heterogeneous in its hereditary make-up that it would most likely not develop at all. In other words, the complexity permitted in the embryo would limit the diversity of hybridization before the dissimilarity in the composition of the food supplied by one parent could have any appreciable effect upon the development of the zygote.

To postulate the origin of endosperm hybridization as an adaptation having survival value, it is necessary to presuppose that it arose in plants which were naturally widely crossed. In such forms the effect of heterozygosis in increasing the amount of endosperm as shown in maize would, no doubt, have been operating. Hence, if it is feasible to account for the origin of double fertilization as an adaptation, it would seem more likely that such a process arose as a means of increasing the *amount* of food supplied to the embryo rather than as a method of adjusting its *composition* to the needs of the developing plant. In all probability both factors help in the early stages of a plant's development. Whether or not it is an adaptation, or whether either of these factors was concerned in the initiation of this puzzling process, I do not attempt to decide.

COULTER and CHAMBERLAIN (**6**) do not distinguish between the fusions of like nuclei and the fusion resulting in double fertilization. They say:

The development and structure of the endosperm of angiosperms is so much like that of gymnosperms that it seems easier to regard the various fusions as merely resulting in a stimulus to growth than to imagine a degenerate embryo assuming this particular development and structure (*loc. cit.* p. 183).

Considering double fertilization as an adaptation means that endosperm hybridization arose as a different process from that of nuclear fusion in which nuclei derived from one individual take part. Of course the union of like nuclei cannot be considered as a means of altering the food supply, so that NĚMEC's hypothesis has no bearing upon this phase of the problem. Neither can the union of like nuclei be a means of increasing the amount of food in the way that endosperm hybridization does, since heterosis, according to the hypothesis recently advanced by the writer (10), is not due to an indefinite physiological stimulus, but merely the result of bringing together the maximum number of growth factors showing partial dominance.[2]

If increased endosperm development is simply a manifestation of heterosis and as such can be put on a Mendelian basis, the process of endosperm hybridization, in so far as it arose as a means of either increasing the amount or altering the kind of food supply, is a phenomenon quite apart from the fusion of like nuclei. Moreover, if double fertilization came about as an adaptation, having occurred in cross-pollinated plants, it must have persisted as a process of no value, both in species which are now almost entirely self-pollinated, as well as in those which do not produce an appreciable amount of endosperm, as NĚMEC points out.

Whether or not heterosis can be removed entirely from the category of results due to indefinite "physiological stimulations," in which category the results of the fusions of like nuclei would still be, remains to be seen. Some interesting results obtained from wheat crosses have an important bearing on the question. Both G. F. FREEMAN[3] of the Arizona Experiment Station and K. SAX[3] of the Washington Experiment Station have obtained independently

[2] The two serious objections to the hypothesis of dominance as a means of accounting for heterosis previously advanced do not hold when the facts of linkage of hereditary factors are taken into consideration.

[3] Unpublished data.

crosses between two distinct types of wheat-macaroni (*Triticum sativum*, var. *durum*) and bread wheat (*Triticum sativum*, var. *vulgare*), which gave seeds much reduced in size and shrunken in appearance as the immediate result of cross-pollination. The smaller size and poor development of the seeds were due to the condition of the endosperm. The embryos were fully developed, however, and the first generation hybrid plants grown from these seeds were in some cases distinctly larger than either parent. This evidence of heterosis was shown in an increase in height of plant.[4] If this hybrid vigor were due merely to a physiological stimulation of cell division it would seem that the endosperm tissue would be stimulated in the same way and show an increased development. On the view that heterosis is due to a bringing together of the greatest number of different favorable growth factors, these results would be easier to understand if it be assumed that the aggregated factors were favorable to the growth of the first generation hybrid plant but not to the hybrid endosperm. Cases of this kind in wheat, which may be rare, however interpreted, would certainly argue against the origin of endosperm fertilization as an adaptive process.

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LITERATURE CITED

1. ANDRONESCU, D. I., The physiology of the pollen of *Zea Mays* with special regard to vitality. Publ. Depart. Agric. Kingdom of Roumania. 1915.
2. COLLINS, G. N., and KEMPTON, J. H., Effects of cross-pollination on the size of seed in maize. U.S. Dept. Agric., Circular 124. 1913.
3. ———, A hybrid between *Tripsacum* and *Euchlaena*. Jour. Wash. Acad. Sci. **4**:114–117. 1914.
4. ———, Patrogenesis. Jour. Heredity **7**:106–118. 1916.
5. CORRENS, C., Bastarde zwischen Maisrassen, mit besonderer Berücksichtigung der Xenien. Bibliotheca Bot. **53**:1–161. 1901.
6. COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of angiosperms. New York. 1912.
7. DARWIN, CHARLES, The effects of cross and self-fertilization in the vegetable kingdom. London. 1876.

[4] In some of the cases the increase in height was shown by actual measurements; in others, observation showed that the plants were at least as well developed as the parents.

8. De Vries, Hugo, Gruppenweise Artbildung. Berlin. 1913.
9. Gärtner, C. F., Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. Stuttgart. 1849.
10. Jones, D. F., Dominance of linked factors as a means of accounting for heterosis. Genetics 2:466–479. 1917.
11. Kölreuter, J. G., Dritte Fortsetzung der Vorläufigen Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. 1766. Reprinted in Ostwald's Klassiker der exakten Wissenschaften. No. 41. Leipzig. 1893.
12. Millardet, A., Note sur l'hybridation sans croisement ou fausse hybridation. Mém. Soc. Sci. Phys. Nat. Bordeaux 4:347–372. 1894.
13. Němec, B., Das Problem der Befruchtungsvorgänge. Berlin. 1910.
14. Shull, G. H., Duplicate genes for capsule-form in *Bursa bursa-pastoris*. Zeitsch. Ind. Abst. u. Vererb. 12:97–149. 1914.

NOTES ON SOME SOUTHERN CALIFORNIA PLANTS

S. B. PARISH

In the following list those plants whose names are designated by an asterisk are here first reported from the state; those marked by a dagger are additions to the known flora of the southern counties. The numbers under which specimens collected by the writer were distributed are inclosed in parentheses without the collector's name; they are represented in the herbaria of California, Harvard, and Stanford Universities.

* CHEILANTHES FEEI Moore, Ind. Fil. 38. 1857.—Providence Mountains, *T. S. Brandegee* (hb. Univ. Cal.). Erroneously reported in Zoe **5**:153 as *Notholaena Newberryi* Eaton.

PILULARIA AMERICANA R. Br. Berlin Monatsb. 1863:435.—Abundant in desiccating winter pools on a clay mesa near Upland, *Ivan Johnston* 34, March 8, 1917. The few previous collections in this state were made near San Diego and Santa Barbara, growing under similar conditions.

ISOETES MELANOPODA PALLIDA Engelm. Trans. St. Louis Acad. 4:387. 1882.—Abundant in the above pools, where it was collected at the same date by the same collector. While the plants are much smaller than indicated in the type character, the longest of the very narrow leaves being not quite 4 cm. long, they agree with specimens collected by *Orcutt* at San Diego and now in the U.S. National Herbarium, which were identified as authentic by A. A. EATON and with which they were kindly compared by Mr. MAXON.

* PASPALUM LARANGAE Arech. Ann. Mus. Nac. Monteved. 1:60. *pl. 2.* 1894.—In ground irrigated by the water tank at Palm Springs railway station, Colorado Desert (8620, September 20, 1913). Mrs. AGNES CHASE, by whom this grass was identified, informs me that there is another specimen in the herbarium of the United States Department of Agriculture, coming from Barrey Creek, Butte County.

PENNISETUM VILLOSUM R. Br. in Fresch. Mus. Sencken. **2**:154. 1837.—Occasional along streets and in waste grounds at Ventura (11020, September 19, 1916) and Santa Barbara.

MUHLENBERGIA REPENS (Presl) Hitchc. in Jeps. Fl. Cal. 111. 1912.—In marshy soil near Upland, *Ivan Johnston*, October 2, 1916. The only other station reported from California is *Coville* and *Funston* 228, from Furnace Creek, Death Valley.

* SPOROBOLUS FLEXUOSUS (Thurb.) Rydb. Bull. Torr. Bot. Club **32**:601. 1905.—On dry gravelly plains at Leastalk (10328, June 3, 1915) and in the adjacent New York Mountains (10237) in the southeastern corner of the Mojave Desert.

* PUCCINELLIA SIMPLEX Scribn. U.S. Dept. Agric. Div. Agrost. Circ. **16**:1. *fig. 1.* 1899.—In damp alkaline soil, Rabbit Springs, Mojave Desert (9799, April 26, 1915).

ELYMUS CINEREUS Scribn. and Merr. Bull. Torr. Bot. Club **29**: 467. 1902.—In dry bottom lands along the Mojave River at Victorville (10558, June 25, 1915). The only other reported California collection is *Elmer* 3662, from Lancaster. Both these stations are in the northwestern part of the Mojave Desert. The type was collected at Pahrump, Utah.

SCIRPUS ROBUSTUS PALUDOSUS (A. Nels.) Fernald, Rhodora **2**:241. 1900.—Entirely filling the large pond formed by the run-off of Postoffice Spring, Panamint Valley (10109, May 11, 1915). Probably this is the sedge reported by COVILLE (Contr. U.S. Nat. Herb. **4**:215) as *S. maritimus* from Saratoga Springs in Death Valley, but no *Scirpus* was found there by the writer in May, 1915, nor was it seen elsewhere in the Mojave Desert, even on the Colorado River; but it is abundant at and below Fort Yuma, and is a troublesome weed in the irrigation canals of Imperial Valley.

CLADIUM MARISCUS CALIFORNICUM Wats. Bot. Cal. **2**:224. 1880.—In a swamp near Upland, *Ivan Johnston*, October 2, 1916. In his description WATSON cites two specimens, one from "a swamp near San Gabriel," and the other from southern Nevada. The only subsequent collection in the state was *Coville* and *Funston* 231, from Furnace Creek, Death Valley. BREWER'S southern California collections were made in 1876, so that 40 years elapsed before the plant was rediscovered in the cismontane region, local botanists

having searched for it in vain, and having come to regard it as extinct, or wrongly attributed to their region. JOHNSTON'S station and BREWER'S are not widely separated.

YUCCA BACCATA Torr. Bot. Mex. Bound. Surv. 221. 1856.—Abundant on mesas and foothill slopes of New York (Barnwell, 10281, June 4, 1915), Ivanpah, and Providence mountains, in the southeastern part of the Mojave Desert. Associated with *Y. brevifolia* Engelm. and *Y. mohavensis* Sargent. From the last species, the acaulescent forms of which it much resembles, it can readily be distinguished by the yellow-green color of the foliage. The plants are acaulescent, or nearly so, in few-branched clumps, the close panicle elevated on a scape not more than a meter high.

PHYLLOGONUM LUTEOLUM Coville, Contr. U.S. Nat. Herb. 4: 190. *pl. 21.* 1893.—Furnace Creek, Death Valley (10008, May 18, 1915). Very sparingly scattered among the pebbles covering the dry bed of the stream, immediately above the small marsh from which the stream rises, probably the exact spot where COVILLE, on April 7, 1891, collected the two specimens on which he founded the genus, since which time the plant had not been rediscovered. Two small specimens were also seen in a dry wash between Furnace Creek and Saratoga Springs. So far as known, the species is an endemic of Death Valley, and very rare even there. The plants are prostrate, and the largest found had stems hardly 3 cm. long.

ATRIPLEX CONFERTIFOLIA Wats. Proc. Amer. Acad. **9**:119. 1874.—This is one of the most widely distributed plants of the Mojave Desert, and often the dominant species, but it has not been found in the Colorado Desert, where *A. canescens* James occupies a like dominance. The latter species is found in most parts of the Mojave Desert, but constitutes a very subordinate part of the plant cover.

* SALICORNIA UTAHENSIS Tidestrom, Proc. Biol. Soc. Wash. **26**:13. 1913.—A small colony on the borders of Panamint Marsh, at a point on the road from Lone Willow Spring to Ballarat (10403, May 9, 1915).

† AMARANTHUS DEFLEXUS L. Mant. **2**:295. 1771.—This amaranth, which is so abundant in the streets of the cities about San Francisco Bay, is equally abundant in the streets of Santa Barbara

(10111c, September 12, 1916), and in June 1917, a few plants were collected along the railway at Ontario (*Johnston* 1433).

* ALLIONIA LINEARIS Pursh, Fl. Am. Sept. 728. 1814. Barnwell, New York Mountains (10276, June 3, 1916), and at the same place by Mrs. *K. Brandegee*. Both specimens are scanty and immature and possibly may prove to be *A. pinetorum* Standley.

† ABRONIA EXALTATA Standley, Contr. U.S. Nat. Herb. **12**:318. *pl. 35*. 1900.—On a dry hillside at Baxter, at the lower end of the "Narrows" of the Mojave River (10403, May 25, 1915). Also at Kelso, in the same desert, *T. S. Brandegee*, June 1915.

CALANDRINIA AMBIGUA (Wats.) Howell, Erythea **1**:34. 1893.—Infrequent in dry alkaline soil. Manix Lake, near Camp Cady, *Shreve*, April 23, 1915. Afton, upper end of the "Narrows" of the Mojave River (10366, May 24, 1915). Salt Springs, in the ancient channel of Amargosa River (10405, May 21, 1915). The type and all other previous collections were from the Colorado Desert.

* SAGINA APETALA Ard. Anamad. Bot. Spec. Alt. 2, *pl. 5*. 1764.—Plentiful in a city yard, Pasadena, *George B. Grant*, April 15, 1917. Plants sparsely glandular, the bases of the leaves not ciliolate. The variety *barbata* Fenzl has been collected in several places in Central California.

BERBERIS FREMONTII Torr. Bot. Mex. Bound. Surv. 30, 1859.—New York Mountains near Barnwell (10258, June 4, 1915), three small groups of scrubby trees 10–12 ft. high.

ARGEMONE INTERMEDIA CORYMBOSA (Greene) Eastwood, Erythea **4**:96. 1896.—Frequent on dry mesas in the Mojave Desert. Black's Ranch, *Hall* and *Chandler* 6848. Silver Lake (9863, May 22, 1915). GREENE's type, as represented on sheet 126416 hb. Univ. Cal., consists of two capsules, and is labeled "M. K. Curran, June 1884, Mojave Desert."

* LESQUERELLA GORDONI (Gray) Wats. Proc. Amer. Acad. **23**:253. 1888.—Abundant, the stems protruding through the low shrubs scattered over the arid mesa at Goffs, Mojave Desert (9647, March 22, 1915). In early June of the same year all traces of the plant had disappeared.

* LESQUERELLA PALMERI Wats. Proc. Amer. Acad. **23**:255. 1888.—A single plant on a dry hillside under pines, Bear Valley,

alt. 6500 ft., in the San Bernardino Mountains, June 18, 1916, *Chandler*. The type of this species was a plant grown at Washington from seeds collected in 1872 somewhere in Arizona by *Palmer*. A second collection was cited from Topo Canyon, Lower California, *Orcutt* in 1884, but I can learn of no later collections.

* STANLEYA ELATA Jones, Zoe **2**:16. 1891.—On dry banks near the head of Wild Rose Canyon, Panamint Mountains (10004, May 14, 1915). Only a few plants were seen, just beginning to flower. The type was collected at Hawthorn, Nevada.

OXYSTYLIS LUTEA Torr. and Frem. Frem. 2d Rept. 313. 1845.—A few specimens were seen in dry soil at several places along the Amargosa River, but only in dry remains (Zabriskie, 9889, May 20, 1915), but living plants were found in the almost obliterated ancient channel of that river near Salt Spring (9877, May 21). The plant appears to be strictly endemic in this limited region.

* LUPINUS FLAVOCULATUS Heller, Muhl. **5**:149. 1909.—Wild Rose Spring, Panamint Mountains (10073, June 3, 1915). Barnwell, *K. Brandegee*. The type was from Nye County, Nevada.

LUPINUS PALLIDUS Brandegee, Zoe **4**:203. 1893.—*L. desertorum* Heller, Muhl **2**:72. 1905.—Randsberg, *Heller* 7679, type of *L. desertorum*. Lone Willow Wash, Argus Mountain (10114, May 9, 1915). Ord Mountain, *Hall* and *Chandler* 6792. The type was from San Vincente, in northern Lower California, and the plant has also been collected in the Colorado Desert.

ASTRAGALUS TRIFLORUS Gray, Pl. Wright **2**:45. 1855.—New York Mountains near Leastalk (10364, June 3, 1915).

TRIFOLIUM GRACILENTUM var. **reductum** Parish, var. nov.—Abundant in coarse decomposed soil, on the summit of Pilot Knob, alt. 5525 ft., Mojave Desert (10160, May 10, 1915). Stems erect, simple or with 1–2 short branches, 4–6 cm. high; leaflets cuneate-obovate, erose, denticulate, strongly nerved, 2–3 mm. long; heads 2–4-flowered; corolla purple, 5 mm. long; pods ~~ovated~~, 2-seeded, 4 mm. long.

CASSIA ARMATA Wats. Proc. Amer. Acad. **2**:136. 1876.—This species, which is abundant in the southwestern borders of the Mojave Desert, has now been collected on the Colorado Desert

side of Eagle Mountains at Cottonwood Springs (10856, May 13, 1916).

RUTA CHALAPENSIS L. Mant. 1:69. 1767.—Abundant for some distance along a street in the Mexican quarter at Ventura (11046, September 1916). The *Ruta bracteosa* of DAVIDSON'S *Plants of Los Angeles County*, reported as found "in a field at El Monte."

TETRACOCCUS HALLII Brandegee, Zoe 5:229. 1908.—Abundant on the arid hills at Cottonwood Springs, in the Eagle Mountains, a part of the range dividing the Colorado from the Mojave Desert (10844, 10845, May 13, 1916). The type was collected, in flower only, at Chuckawalla Bench, in the same region as above, by *Hall* and *Greata* 5865, and the plant is known only from these two collections. A compact rigid shrub 0.6–1 m. high; capsule ovoid to ovoid-oblong, light brown, densely hirsute with very short white hairs, 6–7 mm. high; carpels 3, lobulate at base, 1-seeded; seeds light in color, shining, minutely puncticulate; caruncle minute, wart-shaped.

* CONDALIA LYCIOIDES (Gray) Weberb. in Engl. and Prantl. Nat. Pflanzenf. 35:404.—Forming dense thickets along the edge of the dry wash at Cottonwood Springs (10846, May 13, 1916).

* MENTZELIA NITENS Greene, Fl. Franc. 234. 1891.—In dry washes, Lone Willow Springs, Argus Mountain (10129, May 9, 1915).

MENTZELIA REFLEXA Coville, Proc. Biol. Soc. Wash. 7:74. 1892.—This is a common plant in dry hot canyons in the Panamint Mountains and Death Valley region, where the type was collected by *Coville* and *Funston*. Furnace Creek (10041, May 17, 1915); Salt Creek (10063, May 21). A few specimens were found at Calico (9780, April 23), which is the western known limit.

* OPUNTIA ACANTHOCARPA Engelm. and Bigel.; Engelm. Pacif. R.R. Rept. 4:51. 1856.—An abundant and vigorous growth of this *Opuntia* forms a distinct belt along the base of the New York Mountains near Leastalk.

OPUNTIA MOJAVENSIS Engelm. and Bigel.; Engelm. Pacif. R.R. Rept. 4:40, *pl. 9, figs. 6–8*. 1856.—In 1853 BIGELOW collected a platopuntia "on the Mojave, west of the Colorado," to which the foregoing name was given. In April 1915 I sent living specimens

of an *Opuntia* found in the New York Mountains at Barnwell to ROSE, which he identifies as of this species, which in the intervening years had remained known only from the original imperfect specimens.

OPUNTIA PARRYI Engelm. Amer. Jour. Sci. II. **14**:339. 1852.—Two small clumps of this rare species were seen, June 1915, growing in sandy soil on the open mesa at Leastalk.

* GAURA COCCINEA Nutt.; Pursh, Fl. 733. 1814.—Providence Mountains, *Brandegee*. New York Mountains, near Barnwell (10254, June 4, 1915).

* OENOTHERA MULTIJUGA Wats. Proc. Amer. Acad. **8**:595. 1873.—Two plants of this little known species were collected at "The Tanks" in Furnace Creek, Death Valley (10045, May 18, 1915). The type was from Utah.

* OENOTHERA PRIMIVERIS Gray, Pl. Wright. **2**:58. 1853.—Apparently not infrequent in parts of the Mojave Desert in early spring. Randsberg and Barstow, *K. Brandegee*. Lavic, *Hall* 6103. Goffs (9646, March 22, 1915).

MENODORA SPINESCENS Gray, Proc. Amer. Acad. **7**:388. 1868.—Very abundant on the mesa at Leastalk (10360, June 5, 1915), and conspicuous by the shining white fruit with which the low bushes were plentifully laden. A few taller shrubs were found in flower in the hills 14 miles northeast of Barstow (9795, April 23, 1915). Other collections are: Providence Mountains, *Brandegee;* Argus Mountain, *Hall* and *Chandler;* Ord Mountain, *Hall* and *Chandler*.

* AMOBROMA SONORAE Torr. Ann. Lyc. N.Y. **8**:51, *pl. 1*.—Sandhills near Meloland, Imperial Valley, *W. C. Paccard* in 1914. In May 1915 I saw a specimen on exhibition at Brawley in the same valley, which had been found in the neighborhood. The type was from adjacent Sonora.

GILIA OCHROLEUCA Jones, Contrib. W. Bot. **8**:35. 1898.—The type was collected in the Argus Mountains, and other collections are: Darwin Valley, *Hall* and *Chandler* 7103; Nelson Range, *Hall* and *Chandler* 7113; Barnwell, *T. S. Brandegee;* Kramer, *K. Brandegee;* Rabbit Springs (9807, April 25, 1915). The species appears to be endemic in the Mojave Desert, the Colton specimen cited by BRAND (Engl. Pflanzenr. IV. 250: 105) being an error, as I am informed by JONES, to whom it is attributed.

PHACELIA CALTHIFOLIA Brand, Beitrag. Hydroph. 8. 1911.—An abundant plant in the Death Valley region, growing in gravelly soil in washes and in open ground. Furnace Creek, the type station (10036, May 17, 1915). Zabriskie, on the Amargosa River (10021, May 20, 1915).

* OREOCARYA ECHINOIDES (Jones) Macbr. Contr. Gray Herb. N.S. no. 68. 31. 1916.—A few plants were found growing among the rough rocks at "The Cave" in the Ivanpah Mountains (10243, June 5, 1916).

* LYCOPSIS ARVENSIS L. Sp. Pl. 139. 1753.—Well established in a wash at Upland, *Ivan Johnston* 29, March 3, 1917.

SALVIA FUNEREA, Jones, Contrib. W. Bot. **12**:71. 1908.—A single compact, rounded shrub, about 0.3 m. high, in the dry bed of Furnace Creek, not far from its mouth (10032, May 17, 1915). The type was collected in the adjacent Funeral Mountains, and the plant is known only from that and the present collection; it is probably the same as *S. Greatai* Brandegee, Zoe **5**:219. 1906, known only from the type collection, made by *Hall* and *Greata* at Canyon Springs, in the Colorado Desert; but further material is desirable.

PHYSALIS HEDERAEFOLIA Gray, Proc. Amer. Acad. **10**:65. 1874.—Ravines in the mesa at Leastalk (10362, June 3, 1915) and abundant in the adjacent New York Mountains (10312, June 5, 1915).

* ANTIRRHINUM KINGII Wats. King's Explor. **5**:215. *pl. 21. figs. 1–4.* 1871.—Emigrant Springs, Mojave Desert (10635, May 14, 1915), a single plant.

MOHAVEA BREVIFLORA Coville, Contr. U.S. Nat. Herb. **4**:168. *pl. 17.* 1893.—An abundant plant in dry washes and on canyon slopes in the Death Valley and Panamint Valley region. Lone Willow Springs (10178); Wild Rose Canyon (10085); Furnace Creek (9865); Greenwater Flat (10051); Baxter (10408), all collected in May, 1915. A few plants collected April 23, 1915. by *Shreve*, in Calico Wash, are the most western known.

* PENTSTEMON SUBULATUS Jones, Contrib. W. Bot. **12**:63. 1908.—A few plants, almost out of flower, were found on a dry bank in the Ivanpah Mountains (10317, June 5, 1915), and one or two were seen at Vanderbilt, in the New York Mountains, on the following day.

* IPOMEA HIRSUTULA Jacq. Eclog. Pl. Rar. 1:63. 1811.—In an orange grove at Riverside, *Gordon Surr*, December 1915. In DAVIDSON'S *List of Los Angeles County Plants* (1892), he includes this plant under the synonym *I. mexicana* Gray, but in a subsequent list published in 1896 he substitutes *I. purpurea* Lam., a common and often troublesome weed in southern California. The above is the only, and certainly an erroneous, previous report of the present species in the state.

CUCURBITA CALIFORNICA Torr. ex Wats. Proc. Amer. Acad. 2: 138. 1876.—The type of this species is said to have been collected "at some locality in Sacramento Valley" by Dr. *E. Pickering* on the Wilkes Exploring Expedition in 1841; and in the *Botany of California* (2:40) it is added that a plant "apparently the same" was collected at Carrizo Creek, in the Colorado Desert, by *Emory*, evidently on the Mexican Boundary Survey in 1852. Nothing further was heard of the plant until August 1882, when the writer found a few individuals growing in sandy soil at Redlands, all of which were destroyed in a few years by the advance of cultivation. Material from this collection was described by PARRY in Bull. Torr. Bot. Club 10:50, with a cut of a leaf and section of the fruit. PARRY was the first to point out the real distinguishing characters of the species, for WATSON'S two lines of description is scarcely improved by him in the *Botany of California*, and neither of them suffices to discriminate this from *C. palmata* Wats., a frequent species of the southern California deserts, found also in some cismontane parts of San Diego and Riverside counties, and even reported to reach San Joaquin County in the central California area. The two species are very similar in their general aspect; in fact, on cursory inspection, they might readily be confounded when not in fruit, which may account for the few collections of the rarer species. *C. californica*, however, is readily recognizable at all times by the harsher hispidity of its leaves; but the best character is found in the hispid ovary, and especially in the hispid fruit, which has a thin, soft rind, becoming ashy gray in color and rugosely shrunken at maturity. The "smaller size and diminutive foliage" ascribed to the plant in the description can be found in individuals of either species. To the above stations may now be added:

Cottonwood Springs, in the Eagle Mountains, Colorado Desert (10854, May 13, 1916), where it was growing along a dry wash, and a point on the Colorado River 15 miles east of Searchlight, Nevada, where it was abundant and vigorous in the ill-cultivated field of a squaw man (10413, June 6, 1915). So far as I have been able to ascertain, the stations I have given are all that are known for this plant, and in view of their geographical position and of the insufficient original description, they throw some doubt on the identity of the later specimens with the type.

ACAMPTOPAPPUS SHOCKLEYI Gray, Proc. Amer. Acad. **7**:208. 1882.—In dry gravelly soil, Harrison Flat (10168) and Emigrant Springs (10194), both May 13, 1915. The first of these stations is the "Perognathus Flat" of the Death Valley Expedition Reports, and both are on the Death Valley slope of the Panamint Mountains.

PSILOSTROPHE COOPERI (Gray) Greene, Pitt. **2**:176. 1891.—This species is so abundant on the mesas at Cima and Leastalk (10252, June 1915) that considerable tracts are golden with its showy flowers.

* DYSODIA THURBERI (Gray) Robinson, Proc. Amer. Acad. **49**: 508. 1913.—Quite abundant on a small gravelly bench in the Ivanpah Mountains (10241, June 5, 1915), but not seen elsewhere.

* HYPOCHAERIS GLABRA EROSTRIS Cos. and Germ. Fl. Par.—On a dry clay mesa at Upland, *Ivan Johnston* 77, April 8, 1917. Plants slender; stems unbranched or few-branched; leaves obovoid, entire or few-toothed; heads few-flowered; achenes all truncate. An ecological form of arid soils.

SAN BERNARDINO, CAL.

EFFECTS OF REST AND NO-REST PERIODS UPON GROWTH OF SOLANUM

W. F. GERICKE

That important chemical and physiological changes occur in plants, seeds, and bulbs during their rest period has been shown by several investigations. These investigations have been carried out with a considerable number of plants, seeds, and bulbs. Those studies which concerned themselves with the changes in the composition of the potato have been found of especial interest to the present study because of the light they have thrown upon the importance of the chemical changes in the composition of the tubers on the later physiological activities of the plant.

Briefly touching on some of the literature of rest period studies in which the chemical aspect of the problem was considered, we find that the subject matter resolves itself into three general phases: (*a*) the influence on the permeability of the integument, (*b*) the influence on the chemical changes in the embryo, (*c*) the influence on the reserve food material.

CROCKER (**2**) has explained some of the causes of delayed germination as being due to the resistance of the integument of the seed to water and oxygen. His experiments with *Xanthium* showed very clearly that the long dormant period of one of the embryos was simply a question of the imperviousness of the seed coat. Thus in this case the problem of the so-called rest period resolved itself into the adoption of a method to overcome the resistance of the seed coat and to allow water and oxygen to penetrate the tissues.

ECKERSON (**3**) found that after-ripening processes also involved chemical changes in the embryo. The water-holding capacity and the reaction of the embryonic tissue of *Crataegus*, the species used for the experiment, were found to change during the rest period. Cotyledons and hypocotyls gave different kinds of reactions during the after-ripening processes, due to the results of enzymatic activities.

As early as 1890 JOHANNSEN (5) studied the effects on after-ripening of ether treatment. His work with the chemical changes in the after-ripening of bulbs led him to conclude that the lack of growth or the slow growth of the plant during the so-called rest period was not due to the lack of soluble food. His ether treatment of bulbs decreased the length of the after-ripening period, but he was unable to report any important chemical changes due to the treatment, save that amide nitrogen seemed to have been increased in amount.

MÜLLER-THURGAU and SCHNEIDER-ORELLI (7) conducted an extensive investigation on the chemical and enzymatic changes in potatoes during the storage period. They found that the intensity of respiration was increased by a certain rise in temperature. Respiration likewise was increased with the relative age of the tubers. The increased respiration varied with the sugar content, and active enzymes were present at all stages of the rest period. A certain equilibrium between starch and sugar formation was observed.

APPLEMAN (1) found diastatic activity greater in cold storage potatoes than in those stored at room temperature. After-ripening was found to affect the buds rather than the tubers. The chemical changes of after-ripening concerned carbohydrates chiefly. Proteins, lipoids, organic extractives, and inorganic phosphorus remained constant up to the time of sprouting, and no changes were discernible in the proteolysis of the various nitrogen compounds. Metabolic changes of the proteins began rather suddenly, and were found to be concurrent with sprouting, but were not considered the primary processes of after-ripening.

HOWARD'S (4) work on factors concerned with the rest period is of great interest, both as to the extent of his investigations and as to the bibliography of the subject. His experiments show, as KLEBS (6) had already indicated, that the rest period is not a fixed or unchangeable character of plants, but is instead a condition brought about by internal and external agencies. Both HOWARD and KLEBS concluded that although the morphology of a plant is linked up within the protoplasm and the specific structure of the cells, external conditions are of great importance in determining certain outward forms of plant responses.

In the light of the investigations above mentioned the present experiment was undertaken to ascertain whether any vegetative changes in form would develop in the plants grown from tubers of different rest period duration, and to what extent correlation, if any, could be drawn from changes in the chemical composition of the tubers during the rest period. The experiment was carried out in the greenhouse. Due precautions were observed in order to attain uniform and comparable conditions of moisture, temperature, and culture throughout the length of the experiment. Plantings were made at different seasons of the year to eliminate as much as possible the influence of the variation of climate. The potatoes were planted and grown to maturity in large earthen pots containing 12 K. of a good loam soil. New soil was used for every planting and the tubers were planted to a depth of 3 inches unless otherwise indicated. The harvest of the crop at maturity was at the time when the leaves began to dry and fall, while the water content of the soil was still at optimum condition. As the tables indicate, tubers of various rest period durations were used. Plants were grown from tubers of a continuous no-rest period treatment of several generations, as well as from those of rest period treatment also of several generations. The results obtained are indicated in the tables.

A potato known as the Salinas Burbank was used as the original seed for the experiment. It was cut into two nearly equal parts of 150 gm. weight, and planted. Periods of 10 and 11 days respectively were required for the plants to appear from these two half tubers. Three stalks were produced from one half tuber and four stalks from the other. Rapid growth and strong stalk production characterized these plants. Maturation occurred for the duplicate plants in 86 and 90 days respectively from the time of planting, while the actual growing period from the day of appearance of the plants above ground to the harvest averaged 77.5 days.

Series II were the plants produced from seed taken from the crop of series I and were planted immediately after harvest. In this series the potatoes planted were whole tubers of approximately 100 gm. each. Periods of 62 and 67 days were required for the seedlings to appear in the duplicate pots. In this series one-stalked

TABLE I

No. of series	Rest period in days	Progeny of the seed tubers	Day of planting	Day plants appeared	Time for plants to appear in days	Day of harvest	Growing period in days	Time from planting to harvest in days
I	Winter	Original	Apr. 1	Apr. 9	10	June 25	77	86
I	Winter	Original	Apr. 1	Apr. 10	11	June 28	78	90
II	No rest	Seed of I	June 25	Aug. 26	62	Nov. 26	93	157
II	No rest	Seed of I	June 25	Sept. 1	67	Nov. 30	97	161
III	56	Seed of I	Aug. 20	Sept. 2	12	Dec. 1	89	102
III	56	Seed of I	Aug. 20	Sept. 3	13	Dec. 1	88	102
IV	No rest	Seed of II	Nov. 26	Feb. 10	77	May 22	101	178
IV	No rest	Seed of II	Nov. 26	Feb. 7	74	May 17	99	173
V	No rest	Seed of III	Dec. 1	Jan. 31	62	May 15	105	167
V	No rest	Seed of III	Dec. 1	Feb. 9	71	May 25	104	175
VI	230	Seed of I	Feb. 16	Feb. 23	7	Apr. 28	64	71
VI	230	Seed of I	Feb. 16	Feb. 23	7	Apr. 28	64	71
VII	78	Seed of II	Feb. 16	Feb. 28	12	May 25	76	88
VII	78	Seed of II	Feb. 16	Feb. 28	12	May 23	74	86
VIII	82	Seed of III	Feb. 16	Feb. 27	11	May 25	77	88
VIII	82	Seed of III	Feb. 16	Feb. 28	12	May 20	71	83
IX	No rest	Seed of IV	May 20	July 6	46	Oct. 18	104	150
X	No rest	Seed of V	May 25	July 3	40	Oct. 18	107	147
X	No rest	Seed of V	May 25	July 1	38	Oct. 10	102	140
IV	No. IV replanted		May 25	June 3	9	Sept. 8	97	106
V	No. V replanted		May 25	June 5	11	Sept. 14	101	115

plants were produced, indicating that but one bud germinated and developed from each tuber. The actual growing period of the plants above surface averaged 95 days, while the period of time from planting to harvest averaged 159 days. In this series the old seed tubers were recovered and planted.

TABLE II

No. of series	Rest period in days	Progeny of the seed tubers	No. of stalks per plant	Weight of crop in gm.	No. of potatoes produced per plant
I	Winter	Original	3	491.0	11
I	Winter	Original	4	513.2	13
II	No rest	Seed of I	1	230.8	6
II	No rest	Seed of I	1	208.0	3
III	56	Seed of I	3	300.0	8
III	56	Seed of I	3	263.0	7
IV	No rest	Seed of II	1	437.0	7
IV	No rest	Seed of II	1	409.1	1
V	No rest	Seed of III	1	303.3	3
V	No rest	Seed of III	1	280.5	2
VI	230	Seed of I	5	47.4	11
VI	230	Seed of I	6	50.2	14
VII	78	Seed of II	3	356.0	6
VII	78	Seed of II	4	263.0	7
VIII	82	Seed of III	3	Did not harvest	
VIII	82	Seed of III	3	Did not harvest	
IX	No rest	Seed of IV	1	205.2	2
IX	No rest	Seed of IV	1	287.3	3
X	No rest	Seed of V	1	295.1	2
X	No rest	Seed of V	1	344.2	4

The seed tubers for series III came from the crop of series I which were placed in a closet in the greenhouse and protected from sunlight. The seed consisted of whole tubers of about 100 gm. weight and had a rest period under greenhouse conditions of 56 days. In this series the plants appeared above surface in 12 and 13 days respectively, 3 buds sprouting and developing stalks in each of the pots. The actual growing period of the plants from the appearance of seedlings averaged 88.5 days, while the time from the day of planting to the day of harvest was 102 days.

While the actual growing period of series III was about one week less than that of series II, the most significant effect of the 56 days' rest period of series III was to hasten the germination of the buds of the tubers and to produce plants of several stalks, instead of one, as was the case of the plants in series II. The

after-ripening processes of the potatoes, therefore, proceeded in the soil, but the degree and perhaps the specificity of the processes were different from those occurring in the tubers under ordinary conditions of storage. That the 56 days of rest period did not materially shorten the total time required for the seed potatoes harvested from series I to produce a crop is evident from the fact that the total time required for series II and III to produce a crop from the harvest of the tubers from which they grew, namely, series I, is about the same as indicated in the sum of the rest period and growth period of the two series. The germination of one bud in the tubers of the no-rest period may indicate the localization of the products of the after-ripening processes. The failure of other buds to sprout while the one stalk was growing and maturing a crop could have been due in part to the insufficiency of proper plant food in the tuber. Furthermore, the production of substances by the growing plant which could act inhibitively to the germination of other buds of the tubers may offer a partial explanation for the failure of other stalks to make their appearance. The fact that the seed tubers of the no-rest series remained in the ground for a long time without decay may indicate the presence of some protective agent, or that the condition of the tuber was such as to preclude bacterial decomposition. The probable lack of both sugar formation and the hydrolysis of other food material in the no-rest period tubers may be causes that have not permitted the development of the organisms of decomposition.

In series IV, another no-rest period set, half tubers of 82 and 89 gm. weight respectively were used for planting. The time required for the plants to appear above ground was 77 and 74 days for the duplicate pots. The actual growing period of the visible plants averaged 100 days, and the time from planting to harvest averaged 175 days. Similarly to series II, just one-stalked plants were produced, indicating the germination and growth of one bud for each half tuber.

Series V, another no-rest period set, was planted with whole tubers of 53.6 and 56.9 gm. weight from the crop of series III. The results obtained for this series were similar in all respects to those obtained for series IV, as the results in table III show. The

original seed tubers of series IV and V were recovered, the soil carefully removed, and the potatoes weighed. The results are given in table III.

Series VI was planted with tubers produced from series I. These potatoes were kept in a closet in the greenhouse away from sunlight, but otherwise subjected to practically the same conditions as prevailed in the greenhouse. The rest period of this seed was 230 days. The loss of weight of the potatoes during the rest period was not determined, but the loss was considerable as the

TABLE III

Series	Original weight in gm.	Weight after maturation of one crop in gm.	Loss of weight in gm.
IV.....	82	82	0.0
IV.....	89	88.7	0.3
V.....	53.6	53	0.6
V.....	56.9	Not recovered	

tubers were badly shriveled. The appearance of the seedlings above surface in the form of several stalks occurred on the seventh day after planting. The actual growing period was 64 days, and the period from planting to harvest 71 days. While series VI went through the growth cycle in less time than any other series, the actual production, both as to size of the plants and weight of tubers produced, was much less than that of any other crop of the entire experiment.

Series VII and VIII were planted with tubers from the crops produced from series II and III respectively. The rest period for the seed of the former was 78 days and for the latter 82 days. The plants appeared in 12 days, and the growing period above ground averaged 75 and 74 days respectively, while the time from the day of planting to the day of harvest averaged 87 and 85.5 days respectively. Several stalks per plant were produced in all cases. Series VII and VIII came the nearest of any in the entire experiment to simulating series I, which may be considered the normal series, because it was grown from tubers that had the normal rest period, coming from winter storage.

Series IX and X represent the third and second generations of a continuous no-rest treatment series. The seed potatoes for these series were halved; one part was planted and the other half kept for analysis. The purpose was to compare the analysis of tubers which had produced a crop with that of normal potatoes and thus learn how much of the plant food in the tubers is used in the growth of a crop. The results obtained in series IX and X were similar to those already stated for other no-rest period series. One-stalked plants were produced in all cases. A period of 46 days was required for series IX to appear above ground, while the plants of series X appeared on an average of 39 days. The average length of the actual growing period above ground was 104 days, which is about 4 weeks longer than that of series I, VII, and VIII, the normal ones for this variety of potato.

The seed tubers of series IV and V were recovered and planted as already mentioned. The appearance of the plants above ground from this second planting occurred in 9 and 11 days, which was much less time than that required for their appearance at the first planting. The actual growing period of the plants above surface was 97 and 101 days, a long period, similar in this respect to the case of their first planting. Three to four stalks developed from the tubers instead of one stalk, as was the case in the first crop of this series.

That the growth of some plants can be affected by rest period changes in the composition of its seeds or bulbs has been shown by this experiment with the potato. The most significant effect observed was the variation in the length of the growing period, both as to the length of time required for the plants to appear and the length of the actual growing period above ground. The potatoes planted immediately after harvest to the depth of 3 inches produced one-stalked plants. All of these forms of plant responses undoubtedly were influenced by certain chemical changes in the tuber indicated to some extent by the various investigations mentioned. That the after-ripening changes in the potatoes used in this experiment, because of the conditions imposed upon the seed tubers, may have been affected in the rate, quantity, and specificity of their reactions, seems a reasonable conclusion.

The potato grown from the seed of the normal rest period treatment produced plants of several stalks. Judging from the investigations (1, 7) already referred to, one would expect that in these tubers the products of chemical reactions had approached a certain equilibrium, so that the sugar formation was at its maximum, and conditions were optimum for the activity of the diastatic enzymes. The potatoes planted without rest period treatment could not undergo similar changes as those of the normal rest period ones, as the agency of vegetative growth induced by the peculiar condition under which the tubers were placed would preclude the attainment of a similar chemical equilibrium as that existing in the tubers of the normal resting period treatment.

That not all of the food material in the seed tubers was used in the growth of the plants was shown by the fact that the seed potato, when planted again, germinated, grew, and matured a crop. In the second growth of the tuber several stalk plants appeared above ground in about the normal time. Excepting the fact that the second planting was not carried out with a sufficient number of plants for conclusive results, the results obtained indicated that the after-ripening of the potato, while it grew a crop, did not serve to decrease materially the growing period of the plant for its second growth.

With a more detailed study of the potato by means of the analyses of the seed tubers before and after their plant production, some data may be obtained which may throw light upon this interesting phase of plant physiology.

Summary

1. A study of the effect of various rest periods of the potato tuber upon the subsequent growth of the plants is here reported.

2. After-ripening processes in the potato occurred whether the tubers were in the ground or in ordinary storage.

3. Potatoes planted immediately after the maturation of a crop required a much longer period for the germination of the buds and the appearance of the plants above ground than did potatoes that had a rest period.

4. The no-rest period tubers, when planted, produced one-stalked plants, indicating the germination and growth of one bud.

5. Plants grown from the no-rest period tubers had a longer growing period than did plants grown from the normal rest period tubers.

6. Most of the seed tubers of the no-rest series plants were recovered. These potatoes had lost very little in weight. When these tubers were planted the second time, germination and growth of several buds ensued. The plants appeared above ground in about the same time period required for the plants of the normal rest period tubers. The growing period of the no-rest period plants in the second planting was nearly equal to that of their first planting.

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LITERATURE CITED

1. APPLEMAN, C. O., Study of rest period in potato tubers. Md. Exp. Sta. Bull. 183. 1914.
2. CROCKER, W., Rôle of seed coats in delayed germination. BOT. GAZ. **42**: 265–291. 1906.
3. ECKERSON, S. H., A physiological and chemical study of after-ripening. BOT. GAZ. **55**:286–299. 1913.
4. HOWARD, W. L., An experimental study of the rest period in plants. Mo. Exp. Sta. Res. Bull. 1. 1910.
5. JOHANNSEN, W., Das Ätherverfahren beim Frühtreiben. 2 Auflage Jena. 1906.
6. KLEBS, GEORG, Entwickelungsänderungen bei Pflanzen. Jena. 1903.
7. Müller-Thurgau, H., and SCHNEIDER-ORELLI, O., Kenntnis der Lebenvorgange in ruhenden Pflanzenteile. Flora **101**:309–372. 1910.

FURTHER RESULTS IN DESICCATION AND RESPIRATION OF ECHINOCACTUS

ESMOND R. LONG

(WITH ONE FIGURE)

A description of the results of a series of desiccations of *Echinocactus* carried out at this laboratory has been published, in which changes in the water and carbohydrate balance with the accompanying morphological variations were followed in some detail.[1] The experiments were made under two sets of conditions, some of the plants being desiccated in diffuse light within the laboratory, while others were exposed in the open to the full force of the sun and wind. Besides the characteristic features of the water loss, such as its varying rate under different conditions, and the viability of the plants in the face of prolonged desiccation, a number of interesting discoveries were made as to the fate of the carbohydrate nutriment of the desiccated plants. It was found that Echinocacti drying in the open stored carbohydrate at a rate exceeding its loss, a large portion of the increase taking place in the "soluble non-reducing sugar" fraction (including cane sugar); and that in long desiccation in diffuse light oxidation of the stored sugars took place at such a rate that the dry weight of the plant tissue remained constant, as large a proportion of water being found after 6 years of desiccation in the case of one plant as was present in the beginning, in spite of a loss of nearly 30 per cent of its original weight by water depletion. These results were very striking, and it seemed that it would be of unusual interest to combine these effects in one plant, thereby obtaining new light on the course of katabolism in the various types of carbohydrate and on the time element involved.

Accordingly, an *Echinocactus* which had been loaded with carbohydrate by desiccation in the open, after 8 months was placed in a ventilated dark chamber where photosynthesis was no longer

[1] MACDOUGAL, D. T., LONG, E. R., and BROWN, J. G., Physiological Researches, no. 6, August, 1915.

possible and katabolism would go on without extensive repair. No. 23 of the series referred to was chosen for this purpose, because in treatment, appearance, and amount of water loss it was comparable to no. 22, a plant desiccated in the open, the analysis of which has been recorded. It is entirely probable that in the composition of its tissues no. 23 when put into darkness was similar to no. 22 at the time of its analysis, that is, was characterized by a high content of the sap in soluble non-reducing sugars. The results of the analysis of no. 23 after 22.5 months in darkness are given in table I, in which the corresponding analyses for nos. 7, 22, and 34 are quoted from the article already referred to for comparison. Although it had lost 57 per cent of its original weight in the entire course of its desiccation (12 per cent after it was put in darkness), when removed from the dark chamber it was still of healthy appearance, green at the apex, and only slightly yellowed along the apices of the spiny ridges, and MacDougal ventures the statement that it would have put out new roots had it been returned to the soil in such condition at the proper season.

TABLE I

RESULTS OF ANALYSES OF TISSUES OF *Echinocactus*

Analyses made	No. 23; desiccated in full sunlight 8 months, 10 days and in darkness 22 months, 17 days; total water loss 57.2 per cent		No. 7; desiccated in diffuse light 6 years, 1 month; total water loss 29.3 per cent			No. 22; desiccated in full sunlight 5 months, 6 days; total water loss 40 per cent			No. 34; normal, not desiccated		
Tissue sample.....	ab	c	a	b	c	a	b	c	a	b	c
Dry weight per cent of total weight.....	20.2	17.1	9.5	8.0	5.8	14.3	13.3	11.3	5.8	4.2	3.6
Sap density (water = 1.00).....	1.018	1.035	1.010	1.018	1.013	1.016	1.027	1.034	1.013	1.011	1.011
Sap acidity, N/10....	0.600	0.400	0.144	0.104	0.148	0.244	0.208	0.156	0.172	0.156	0.128
Total hydrolyzable carbohydrate; per cent of total solids..	31.5	28.2	22.3	24.2	11.1	44.3	44.2	43.4	32.3	35.7	29.6
Total reducing sugars; per cent of total sap weight.....	0.08	Trace	0.09	0.06	0.04	0.15	0.13	0.10	0.53	0.42	0.10
Total non-reducing sugars; per cent of total sap weight ...	Trace	Trace	0.11	0.10	0.06	1.28	1.48	2.67	0.14	0.03	0.05

In table I, *a*, *b*, and *c* represent certain arbitrarily defined tracts in the cortex of the plant, *a* and *b* (joined in the case of no. 23)

including the white pulp within the spiny ridges, *a* being the outer sample taken from the area just under the cuticle, *b* being just interior to *a*, while *c* represents the great body of the deeper pulp and is characteristic of nine-tenths of the cortical tissue. The sugar analyses were made with Fehling's solution, calculations being made in terms of dextrose. Reducing sugars were determined by direct titration of the neutralized sap, soluble non-reducing sugars similarly after one hour's hydrolysis of the sap on the water bath with 10 per cent HCl, and total hydrolyzable carbohydrates of a given weight of tissue after 4 hours' hydrolysis with 5 per cent HCl. The last term thus covers all substances which break up with 5 per cent HCl to give reducing sugars, consisting in this instance of a variety of polysaccharides, including pentosans and probably hemi-celluloses as well as starch, besides the soluble sugars. In a rough way it measures the stored nutriment of the plant. A more detailed description of the methods used is given in the previous article.

The results of the observation of no. 23 and of its final analysis are shown in fig. 1 and table I, and the conclusions to be drawn from them may be summarized briefly as follows. As would naturally be expected, the curve of water loss shows a distinct break at the point where the plant was transferred from the rigorous conditions of the laboratory court to the more equable conditions of the dark chamber. A more interesting finding is the uniformity of the rate of the water loss, which, in the already well desiccated plant, seemed almost independent of seasonal changes. Small variations did indeed occur, but they cannot be well shown on the scale of the accompanying tracing. Inasmuch as the temperature variations of the surrounding air must have been large, the dark chamber being located in an unheated portion of the laboratory building, the strong influence of light upon evaporation is shown, for very noticeable seasonal changes in evaporation were observed in other plants drying at fairly equable temperatures even in the diffuse light of the laboratory.

Several distinct changes have taken place in the sugar concentration. A high acidity is noted, which is explained by the conditions of the plant's confinement. It has been repeatedly brought

out at this laboratory that the oxidation of the organic acids resulting from sugar katabolism is more rapid in the presence of light, and that these acids tend to accumulate in darkness. Soluble sugars in no. 23 have been burnt out almost completely, only traces being found in the expressed sap. If, as we have assumed, a high

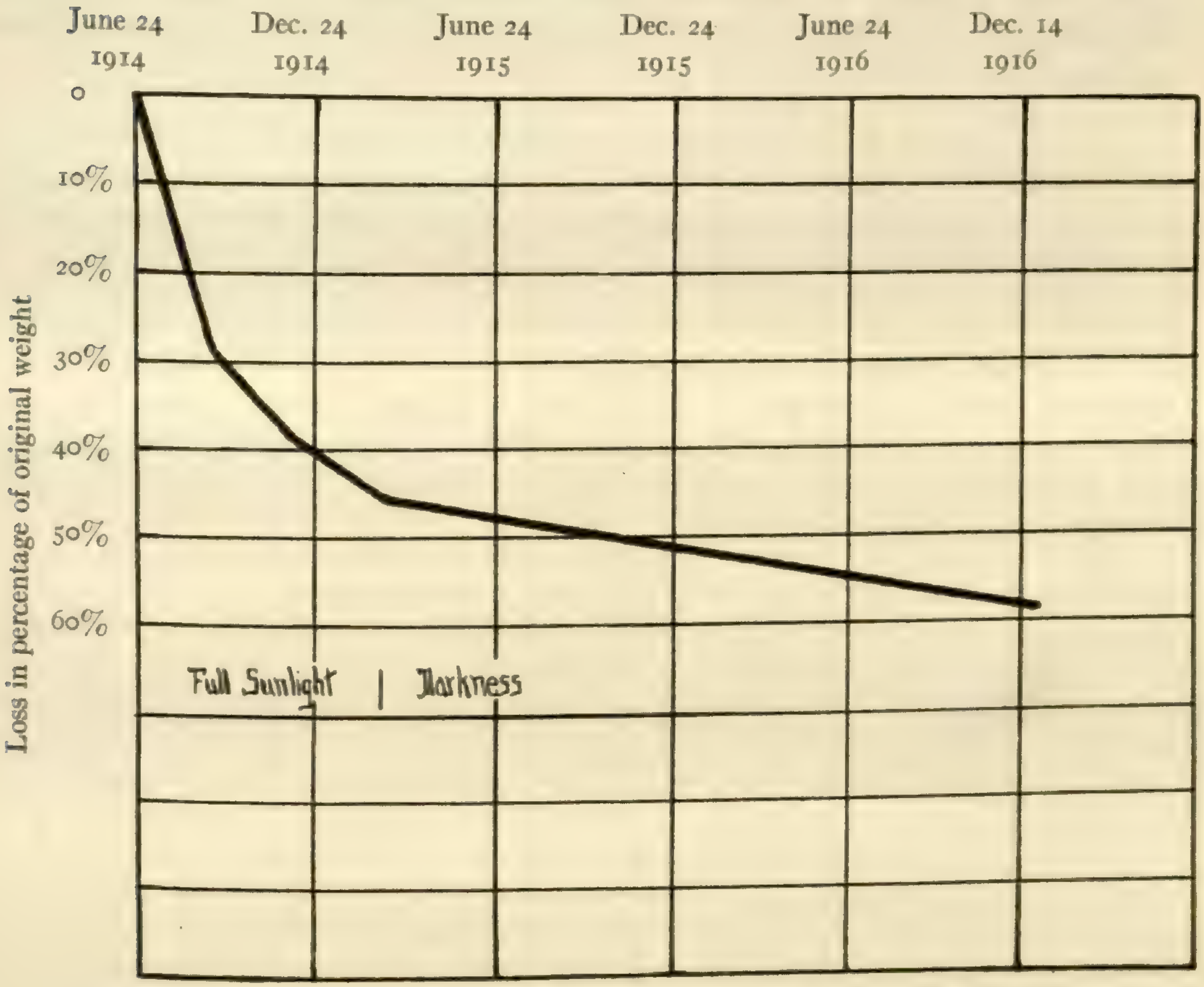

FIG. 1.—Illustrating course of loss in weight of *Echinocactus* no. 23 from June 24, 1914, to January 23, 1917.

concentration of soluble non-reducing sugars was present in the sap of no. 23 at the time when it was put into darkness, a very large destruction has taken place of sugars of this type. However, and this is an important point, the destruction of the stored insoluble polysaccharides seems hardly more than begun. A consideration of table I shows that the total hydrolyzable carbohydrate content of no. 23 after its prolonged stay in darkness is hardly less than that

of the normal, no. 34, and while it is lower than that recorded for no. 22, it must be remembered that the high figure for total hydrolyzable carbohydrates in no. 22 is due in a large measure to the high concentration in the pulp of soluble non-reducing sugars, the term "total hydrolyzable carbohydrates," as defined, covering hydrolyzable carbohydrates of all types, soluble and insoluble. On the other hand, we know that the insoluble polysaccharides of this type do break down in the course of long confinement without photosynthesis; witness the difference in the figures for total hydrolyzable carbohydrate in the case of the normal, no. 34, and no. 7, which rested in diffuse light more than 6 years. Much of the polysaccharide content of no. 7 has evidently disappeared in the course of its starvation; yet what happened to no. 7 in 6 years in diffuse light has not happened to no. 23 in 22 months in darkness. The breaking up of the stored insoluble polysaccharides in response to the plant's demands on its source of energy evidently takes place very slowly, and this fact, taken in conjunction with that of the resistance of the Echinocacti to desiccation, helps in a large measure to explain the viability of these plants in spite of prolonged starvation.

DESERT LABORATORY
TUCSON, ARIZ.

BRIEFER ARTICLES

GROWTH OF TREES IN SPHAGNUM[1]

Data obtained from the Puget Sound region and Alaska indicate that trees grow very slowly in sphagnum. In the habitats examined, there is no soil in the ordinary sense. The surface of the substratum consists of living sphagnum moss, just beneath which is fibrous brown peat. At greater depths decay is complete. The observations reported in this paper were all made on trees growing at an elevation of less than 750 m. Coniferous trees are more common in sphagnum than broad-leaved trees. Table I gives growth data for conifers in sphagnum and in other habitats in the Puget Sound region.

TABLE I

AVERAGE GROWTH OF CONIFERS IN SPHAGNUM AND IN OTHER HABITATS

SPECIES	SPHAGNUM		OTHER HABITATS		PERCENTAGE
	Number of specimens examined	Average annual increase in diameter	Number of examined specimens	Average annual increase in diameter	
	Diameter				
Tsuga heterophylla	13	1.01 mm.	7	1.56 mm.	64
Pinus monticola	9	0.78	11	1.34	58
Thuja plicata	11	0.60	6	1.15	52
Pinus contorta	9	0.78	21	1.57	49
Pseudotsuga taxifolia	21	0.86	16	1.69	40
	Height				
Tsuga heterophylla	11	7.37 cm.	7	17.07 cm.	43.1
Pinus monticola	9	5.39	11	8.62	62.5
Thuja plicata	11	6.45	6	18.55	34.7
Pseudotsuga taxifolia	21	6.32	16	20.93	33.1

The percentage for each species in the last column is obtained by dividing the number in the second column by that in the fourth, and therefore represents, on a percentage basis, the average amount of growth in sphagnum for the specimens examined as compared with the average growth on other soils.

[1] For more complete data, discussion, and literature, see *Jour. Forestry*, **15**: 726–739. 1917.

The data on the growth of conifers in substrata other than sphagnum represented in table I were secured mainly from logged-off lands where natural reforestation was going on. All of the data for lodge pole pine and white pine, and most of those for Douglas fir, were obtained from trees growing on stony, infertile soils. A few of the Douglas firs, all of the hemlocks, and nearly all of the cedars from which data were obtained were growing on somewhat better soils, but in no case on the best class of forest soils. The data were all from young trees.

Data by foresters for larger numbers of older trees growing under the best forest conditions show much more rapid growth in all cases. Table II compares the data of the foresters with those of the writer.

TABLE II

GROWTH OF CONIFERS IN DIAMETER OUTSIDE OF SPHAGNUM; COMPARISON OF DATA OF OTHER WORKERS WITH THOSE OF WRITER

Species	Data of other workers	Data of writer	Ratio
Tsuga heterophylla.....	3.60	1.56	2.3
Pinus monticola.....	4.68	1.34	3.5
Pinus contorta.....	4.80	1.59	3.0
Pseudotsuga taxifolia.....	9.43	1.69	5.5

Differences in the character of the soil, the amount of moisture in soil and air, and the age of the trees are doubtless among the most important factors in producing the higher rate of growth found by the foresters. The comparison merely emphasizes the fact that these conifers, even when under the most unfavorable conditions outside of sphagnum, grow considerably more rapidly than they do in sphagnum. The ratios of growth observed by the writer in sphagnum to that observed by the forestry workers under the best forest conditions is as follows: western hemlock 0.27, western white pine 0.166, lodge pole pine 0.163, Douglas fir 0.091.

It appears from these data that the western hemlock comes nearer to its normal growth in sphagnum than any other species. The ratio of its rate of growth in diameter in sphagnum to its growth in other habitats is greater than that of any other species in the regions examined. In the ratio of its growth in height in sphagnum to that not in sphagnum it is surpassed by the western white pine only. The largest specimen found growing in sphagnum has a height of 12 m. and a diameter of 45 cm. near the base. Several others have been found that approximate this in size.

It is the commonest tree in sphagnum in the Puget Sound region, individuals varying in size from 6 m. down to mere seedlings being common in nearly every sphagnum area examined. Many of the specimens, however, have some dead branches, commonly near the top. The trunks of the larger specimens show the distinctly conical form common in trees growing in sphagnum, indicating that the stunting in height is greater than that of the diameter near the base.

The Douglas fir is seldom found in sphagnum in the Puget Sound region, although it is the most abundant tree in the bordering forests. It is the lowest of the 5 species in the ratio of its growth in both diameter and height in sphagnum to that in other habitats. The largest specimens found in sphagnum are 2 m. high. Seedlings are not abundant. In so far as any conclusions can be based on these data, the western hemlock grows best in sphagnum and the Douglas fir poorest.

The other three conifers mentioned are intermediate between these two. Seedlings of giant cedar are abundant and a few trees reach a height of 5 m. The two species of pine mentioned are found in but few sphagnum areas, but occasionally an area is found in which one or the other of these species has succeeded far better than any other conifer. The Sitka spruce is a common constituent of Puget Sound forests in many places, but has been seen by the writer in only one sphagnum area.

The trees growing in sphagnum in the Puget Sound region are all erect, none being prostrated by bog conditions. That the conifers, at least, are well rooted in sphagnum is indicated by the fact that none of them are found uprooted by wind, although exposed specimens of the same species but little larger are commonly uprooted in other soils.

The only deciduous trees found by the writer in sphagnum in the Puget Sound region are red alder (*Alnus oregana*), bog willow (*Salix myrtilloides*), western dogwood (*Cornus occidentalis*), and the peat bog birch (*Betula glandulosa*). Even these are rare, and all of them except the first are so small as to be considered shrubs rather than trees.

In the forested portions of the Alaska coast some conifers are found in sphagnum. The ones most commonly found are lodge pole pine, Alaska cedar (*Chamaecyparis nootkatensis*), and Sitka spruce. These grow poorly in sphagnum. They are much distorted and are frequently sprawlingly prostrate, although they maintain their erect position and show much better growth in the neighboring forest on ordinary soil.

Along the south coast of the Alaska peninsula, where the sphagnum occurs in the forestless regions, deciduous trees and shrubs are often found in sphagnum. They are usually much stunted and in a great many

cases they are prostrate. The species found are paper birch (*Betula papyrifera alaskana*), peat bog birch, late alder (*Alnus sinuata*), and net-veined willow (*Salix reticulata*).

Toxicity of the substratum is evidently a large factor in the stunting of trees in sphagnum, although several other factors are partly responsible.—GEORGE B. RIGG, *University of Washington, Seattle, Wash.*

PROTHALLIA OF LYCOPODIUM IN AMERICA

Recently I described in this journal (**63**: 66–76. 1917) the prothallia of 5 species of *Lycopodium* found near Marquette, Michigan. In that article (p. 71) I mentioned the difficulty in distinguishing between the prothallia of *L. complanatum* and those of *L. obscurum*, and a footnote was inserted to attempt to clear up a doubtful situation. In the paper, fig. 13 is named *L. obscurum*, but in the light of what follows it is evidently *L. complanatum*.

On May 27, 1917, I found several prothallia which suggested that I had not correctly identified those of *L. obscurum*. Upon following up this suggestion, on August 29 I found a small patch of sporelings of this species, and secured some 30 gametophytes with and without sporelings. They are of the *L. annotinum* type and not of the *L. complanatum* type, as stated in my paper. The excuse for the error is that hitherto the prothallia of *L. obscurum* were unknown; those of *L. complanatum* do not all grow in the same position, nor are they alike in size and color; and finally, the young sporelings of the two species are very similar.

An illustrated account of the sporeling and gametophyte of *L. obscurum* will be given in a later paper.—EARLE AUGUSTUS SPESSARD, *Marquette, Mich.*

CURRENT LITERATURE

BOOK REVIEWS

Anatomy of woody plants

When one reads DEBARY'S classic *Comparative anatomy of the vegetative organs of the phanerogams and ferns*, he finds exceedingly little of a comparative nature, but for the most part an extensive array of facts. In JEFFREY'S[1] work, now before us, we have an eminently comparative view of the subject, although the word comparative is not emblazoned on the title page. No book appearing in recent years better reflects the progress which has been made in this branch and the change in our point of view which has occurred. The rapid rise of a real comparative anatomy of vascular plants is due mainly to two causes: (1) new methods of technique, for which our author is largely responsible, and (2) the notable development of paleobotany, in which our author has had no mean share. At last we have a book in which existing and fossil plants stand side by side as illustrations of the principles which are discussed.

When it became known that JEFFREY had written a book on plant anatomy, we looked for a work characterized by freshness and individuality, and we have not been disappointed. As to the point of view of the author, we find, as was to be expected, that the keynote is not physiology nor histology, but phylogeny. Facts which have no general bearing have only passing interest for the writer, as is illustrated by the statement (p. 126) "on account of its relatively slight phylogenetic interest the epidermal tissue will receive small attention in the present connection." We may here see an explanation of the omission of any treatment of the subject of periderm, which would seem to be a suitable topic for introduction into a work on woody plants.

One of the first impressions which one receives upon opening the book is the number, excellent quality, and originality of the illustrations. The figures, numbering over 300, are mostly from photomicrographs by the author, which sufficiently vouches for their quality. The drawings by R. E. TORREY and others are well executed and clear. A minor matter, except to the teacher of junior students, is the lack of uniformity in the orientation of the figures, as may be seen by comparing figs. 11, 32, 42, also 252 and 253, which face one another. As a piece of book making the work is a credit to the publishers, and there is a remarkably small number of typographical errors. The style of

[1] JEFFREY, E. C., The anatomy of woody plants. pp. x+478. University of Chicago Press. 1917.

treatment of the various topics resembles a lecture illustrated by lantern slides; this is manifestly conducive to clearness. The entire absence of bibliography is a noticeable feature. Probably the introduction of references was not regarded as suitable to a textbook, but still is to be deplored, for it detracts from the usefulness of the book. This omission might well be remedied in a future edition.

A great deal of stress is laid on the three so-called "canons of comparative anatomy," which are stated to be the doctrines of recapitulation, conservative organs, and reversion. In another place the author has neatly expressed the idea thus: "recapitulation, reversion, and retention . . . . are the three R's of biological science." In view of the attacks by zoölogists on the doctrine of recapitulation, and of the confident explanation of reversion by thoroughgoing Mendelians, it is pleasing to find that a botanist who has made a comprehensive study of plant forms not only adheres to these somewhat discredited concepts, but accords them fundamental value. It should be noted that JEFFREY does not deal with "reversion on crossing," but reversion as the result of some stimulus such as wounding, thus bringing into play a new weapon which is a true sort of experimental morphology.

Turning to the arrangement of the topics, the first 10 chapters deal with the various tissue systems, and here naturally the vascular tissues receive the major share of attention. Chapters 11 to 16 consider the organs of the plant, including interesting chapters on the sporangium, which the author argues is an organ *sui generis*, and on the same footing with root, stem, and leaf. Chapter 17 lays down the general principles or canons previously mentioned. The groups Lycopsida and Pteropsida, first distinguished by the author, are next defined, and 11 chapters are devoted to a discussion of the subdivisions of these great groups. A valuable chapter on anatomical structure and climatic evolution follows. The book closes with a concise description of the technical processes involved in preparing woody tissues for study, many of which processes have been devised or improved by the author himself. This chapter does not contain a description of microscopes and other appliances that nobody learns to use from book directions, but proceeds at once to describe the special technique for woody material. A perusal of these 25 pages shows why JEFFREY gets better sections than PENHALLOW obtained by means of a carpenter's plane.

The book would do good service if it merely served to correct some deep-seated fallacies which the author exposes with much skill; for instance, the term medullary ray, the so-called primary rays of oak, the origin of the ring of vascular bundles found in the stem of *Pteris*, the supposed primitive nature of the herbaceous type. It is safe to say that this work should prove useful alike to the paleontologist, the morphologist, and the general student, and should promote the study of plant anatomy in our higher institutions, where the subject has suffered from the lack of a work presenting the subject from a modern point of view.—M. A. CHRYSLER.

British grasses

The necessity of increasing the production of foodstuffs in the British Isles has brought about a considerable reduction in the area of grassland. To offset these reductions, efforts have been made to improve the remaining grassland in order that it may carry a correspondingly larger number of stock. With this in view ARMSTRONG,[2] of the School of Agriculture, Cambridge University, has prepared a comprehensive work on British grasses. The book is divided into two sections, the first being devoted to botany, the second to agriculture. In the botanical section is considered the morphology and "biology" (germination, pollination, and dissemination) of grasses, followed by a detailed description of the species. The author has distinguished the more common grasses by one key, or rather a synopsis, based upon foliage characters, and by another, based upon floral characters. These keys from the standpoint of technique leave much to be desired. They are not dichotomous nor are the characters uniformly contrasting, nor is there uniformity in the method of expression, the style shifting from phrase to sentence ("awn not exceeding palea" set against "awn exceeds palea"). The structure of the spikelet is clearly set forth and well illustrated by diagrams. The figures are nearly all original and in the main are very satisfactory for diagnostic purposes. Some of the half tones are smudgy, but the cuts from drawings are good.

The agricultural section deals with the species from the agronomic standpoint. The commercial grasses of the United Kingdom include about the same species that are used in the cool humid sections of the United States, that is, the states east of the Great Plains and north of Tennessee and Virginia. In this region one meadow grass, timothy, and one pasture grass, Kentucky bluegrass or June grass, stand out preeminently. Redtop (*Agrostis alba*) is important in moist and so-called acid soils, but does not approach the others in acreage or value. Orchard grass and meadow fescue are locally important but fall far behind redtop in acreage. All other grasses for permanent pasture or meadow are, on the basis of acreage and value, scarcely worth considering.

One of the first things the American agronomist wishes to know in consulting a work on British grasses is, what is the relative importance of the different species from the commercial standpoint as indicated by acreage under cultivation or by the value of the product? An answer to this question cannot easily be obtained from the work before us. Apparently there are several species of approximately equal importance. The moist cool climate of the British Isles is favorable for the growth of several species that do not thrive under the more trying climate of the northeastern United States. Besides the species mentioned as important in this country, the following are considered in the present volume in such a way as to give the impression that they are commercially valuable: meadow foxtail (*Alopecurus pratensis*), sweet-scented

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[2] ARMSTRONG, S. F., British grasses and their employment in agriculture. 8vo. pp. viii+199. *figs. 175*. Cambridge University Press. 1917.

vernal grass (*Anthoxanthum odoratum*), yellow oat-grass (*Avena flavescens*), tall oat-grass (*Avena elatior* or, in the botanical section, *Arrhenatherum avenaceum*), crested dog's-tail (*Cynosurus cristatus*), sheep's fescue (*Festuca ovina*), red fescue (*F. rubra*), perennial rye-grass (*Lolium perenne*), Italian rye-grass (*L. italicum*), wood meadow-grass (*Poa nemoralis*), and rough-stalked meadow-grass (*P. trivialis*). All these species are advertised by our seedsmen, but only three, tall oat-grass and the rye-grasses, are used in the United States in more than an incidental way.

The common names are of interest. The species have for the most part retained the English names when grown in this country, but *Agrostis alba*, known in England as bent-grass, is called here redtop; English fine bent-grass (*Agrostis vulgaris*) is called here Rhode Island bent; English cock's-foot is called here orchard grass; English smooth-stalked meadow-grass is called here Kentucky bluegrass or June grass; timothy in England has the alternative name cat's-tail grass. *Cynodon Dactylon*, our familiar southern pasture grass known in the United States as Bermuda grass and in the English West Indies as Bahama grass, is called in England creeping finger-grass. This assumes no agronomic importance there, as the climate is too cool and moist for its best development.

The author is director of the United Kingdom Seed Control Station, a fact reflected in the prominence given to data concerning the seed of grasses. There are two chapters devoted to the subject, one on the valuation and purchase of grass seeds, and one on the specification and compounding of grass seed mixtures. In the botanical section there are cuts illustrating the "seed" (usually the florets) of the commercial species and of the common weed seeds found as impurities in grass seed.

The work is a valuable résumé of British agrostology and should be in the hands of all interested in that subject. However, the problems of grass culture in America are so different from those considered by ARMSTRONG that agrostologists in this country will receive little aid. Our problems have to do with the cultivation of grasses under conditions practically unknown in the British Isles.—A. S. HITCHCOCK.

NOTES FOR STUDENTS

Biology of rusts.—Among recent publications on rusts, GASSNER'S[3] account of his extensive studies in Uruguay gives the first comprehensive picture of the grain rust vegetation of that part of the world. Although the investigations were mostly made in the neighborhood of Montevideo, the observations and

[3] GASSNER, G., Die Getreideroste und ihr Auftreten im subtropischen östlichen Südamerica. Centralb. Bakt. II. **44**:305–381. 1915.

———, Untersuchungen über die Abhängigkeit des Auftretens der Getreideroste vom Entwicklungszustand der Nährpflanze und von äuseren Faktoren. *Ibid*. II. **44**: 512–617. 1915.

conclusions are applicable not only to Uruguay but also to the adjoining province of Buenos Aires in Argentine, whose climate is similar to that of Uruguay. The geographical and ecological aspects of the subject are presented in two papers. The first deals with the species and biological races of grain rusts in the region under consideration, and with their seasonal distribution. The second treats of the influence of external factors on the occurrence of rusts. Of this long account only the salient features can be noted.

Only 4 species of grain rusts occur in the La Plata region of South America. These are *Puccinia graminis*, *P. triticina*, *P. coronifera*, and *P. Maydis*. *P. graminis* infects strongly wheat, barley, and *Lolium temulentum;* less virulently oats. *Lolium perenne*, *Dactylis glomerata*, and *Alopecurus pratensis;* while rye, European oats, *Lolium multiflorum*, and *Phleum pratense* are rarely infected. On other grasses it is not found. From cultures which seemed to indicate that this rust could be transferred from wheat to barley, and from rye, oats, barley, *Lolium temulentum*, and *Dactylis glomerata* to wheat, the author is inclined to believe that only a single biological race is present, which in its choice of hosts does not coincide fully with any of the established races. Although others have noted variations in the degree of fixity of biological races of rusts in different regions, it may nevertheless be assumed with reasonable certainty that further study will reveal more than one specialized form in the La Plata region, and that forms as distinct in other regions as that on wheat on the one hand, and that on oats and *Dactylis glomerata* on the other, will not be found to be identical in Uruguay. With regard to the occurrence of *Puccinia graminis* on the grain crops, it was found that the fungus was generally absent from both wheat and barley during the winter and spring. Some years wheat is entirely free from this rust, and in general the plants are not attacked until they are nearly mature, so that this rust is of little economic importance in the culture of wheat. It is the only rust that occurs on barley. Rye and oats are rarely attacked, but the native variety of oats suffers more severely than imported European types.

Puccinia triticina occurs only on wheat and rye. It is found on wheat in the fields at all times of the year, and on plants of all ages, except in the earliest stages of growth. Infections on rye are rare and only uredospores are produced. The opportunity to prove by cultures and observations that this rust occurs on rye was unusually favorable, because *P. dispersa*, with which it might be confused, does not occur in the La Plata region.

Puccinia coronifera was found on *Avena sativa*, *A. fatua*, *Lolium perenne*, *L. temulentum*, and rarely on *L. multiflorum*. The biological race on oats is different from that on *Lolium*. A striking difference in susceptibility exists between native oats and European varieties. The native type is only lightly attacked, while the European varieties are entirely destroyed, so that their cultivation in this region is impossible.

Puccinia Maydis occurs in Uruguay only on maize, and not on sorghum. Maize is usually planted from October to January, and the rust begins to

appear in December and January. The infection, however, is not sufficiently severe to cause perceptible damage to the crop.

In the second paper, dealing with the influence of external conditions on the occurrence of rust infection, the author points out that in dealing with problems of this kind it is necessary to take into consideration the effect of the state of development of the plant itself. In regard to this question he finds, as others had noted, that, within wide limits, the age of plant organs has little to do with their susceptibility to infection by uredospores and aecidiospores, but that there is, nevertheless, an age limit beyond which infection does not take place. This limit GASSNER finds coincides with that stage of development of an organ at which teleutospore formation begins. Leaves and stems on which the production of teleutospores has begun are no longer capable of infection. This period varies with different rusts. For example, leaves which are producing teleutospores of *Puccinia triticina*, and hence no longer capable of infection by that fungus, can still be infected by *P. graminis*, since teleutospores of *P. graminis* are produced on leaves which have reached a more advanced stage of maturity than those on which teleutospores of *P. triticina* are produced. A peculiar condition of immunity of seedlings of wheat, rye, and oats to the attacks of *P. graminis* was observed. Seedlings of these plants are infected only from January to April. For *P. triticina* and *P. coronifera* and *P. Maydis* no such immunity for the young stages of the host plants was observed. These facts make it imperative that in a study of the influence of seasonal and climatic conditions on the occurrence of rust, only plants of the same state of development should be compared. This condition was met by the author by sowing the various grains at regular intervals throughout the year, so that practically all stages were available for observation at all seasons. The results of this long series of observations can barely be mentioned. It should be stated, however, that the indefiniteness of the results indicates that the problem cannot be settled by observation alone, and that an experimental analysis with control of all the factors involved is necessary before the effect of the individual constituents of the environment can be determined. In general GASSNER believes that the environment acts not directly on the fungus itself, but indirectly through the effect on the host. He finds that the yearly seasonal changes do not affect the occurrence of these 4 grain rusts alike. *P. graminis* is found from the beginning of summer to the beginning of winter; *P. triticina* and *P. coronifera* are to be found producing new infections at all seasons; while *P. Maydis* occurs from midsummer until autumn. A favorable effect of high relative humidity for rust development could not be observed, for the period of highest relative humidity, the winter, was also the period of least rust development. It is, of course, a question to what extent the effect of humidity was obscured by other factors, especially low temperature. In general, high temperatures appear to influence the host plant in such a way as to favor rust development, but isothermal periods in spring and in autumn are not characterized by equal intensity of rust development. It may be a matter

of considerable significance to agriculture that the addition of fertilizers does not increase the susceptibility of the grains to rust infection. High moisture content of the soil was favorable for rust development. Slope and drainage consequently had an influence only in so far as the soil moisture content was affected thereby.

A more direct attack upon the problem of the influence of environmental factors on the development of rusts was undertaken by MAINS.[4] In his work the effect on *Puccinia coronata* and *P. Sorghi* of a number of factors, partly external and partly internal to the host, was studied under controlled conditions. It was found that low temperatures (13–15°) retard the development of these rusts, and that there is also an upper limit in the neighborhood of 30° beyond which growth of the parasite does not take place. Both wet soil and a saturated atmosphere favor the development of rusts, to the highest degree when both factors are present simultaneously. Absence of any of the mineral elements necessary for plant growth does not prevent infection, but decreases the number of pustules produced. The light relations are of special interest as giving an indication of the mode of nutrition of rusts. Light as such is not necessary for the development of the parasite; if, however, the host has been depleted of carbohydrates by being kept in the dark, no rust development takes place. Light, therefore, acts indirectly in so far as it is necessary for the production of carbohydrates for the nourishment of the fungus. For the same reason, rust does not develop in the absence of carbon dioxide on plants which have been deprived of carbohydrates. *Puccinia Sorghi* develops in the dark on sterile seedlings of *Zea Mays* and upon pieces of leaves supplied with solutions of starch, cane sugar, dextrose, maltose, and dextrin, but is not able to grow upon these substances directly. From these interesting experiments the author concludes that rusts are dependent for their nourishment upon some of the intermediate products of carbohydrate metabolism in leaves.

In continuation of his observations on the wintering of rust fungi, TREBOUX[5] reports a number of cases in the vicinity of Riga of the hibernation of rusts by means of a persistent mycelium. The observations were made in February, March, and April, when the melting snow had uncovered the host plants, and before infection from external sources had been possible. When the host plants were brought into a warm room further development of unopened sori was observed in *Puccinia dispersa* on *Secale cereale* and *S. montanum*; *P. obscura* on *Luzula pilosa* and *L. campestris*; *P. arenariae* on *Moehringia trinervia*; *P. Poarum* on *Poa pratensis* and *P. annua*; *P. agropyrina* on *Agropyrum repens*; *Uredo Airae* on *Aira caespitosa*; and *Thecopsora Pirolae* on *Pirola rotundifolia*. In addition to these, field observation showed the

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[4] MAINS, F. B., The relation of some rusts to the physiology of their hosts. Amer. Jour. Bot. **4**:179–220. *pls.* 2. 1917.

[5] TREBOUX, O., Überwintering vermittels Mycels bei einigen parasitischen Pilzen. Mycel. Centralb. **5**:120–126. 1914.

development of uredinia in early spring from persistent mycelia of *Puccinia glumarum* on *Secale cereale; P. coronata* on *Agrostis vulgaris* and *Agropyrum repens; P. Carduorum* on *Carduus crispus; Uredo Festucae* on *Festuca ovina;* and probably also of *Melampsora Lini* on *Linum catharticum*, and *P. bromina* on *Bromus mollis*.

In the neighborhood of Vienna, HECKE[6] finds that, as ERIKSSON and HENNING have occasionally observed in Sweden, *Puccinia glumarum* sometimes persists through the winter by means of hibernating mycelium in the leaves of wheat. In 1914, rust pustules were observed in abundance on the old leaves in March, and from that time the rust was present continuously. No such interruption of continuity between the spring outbreak and the summer outbreak as was reported by ERIKSSON was observed. An abundance of wintering mycelium the author regards as one of the conditions determining the occurrence of rust epidemics or "rust years."

Brief notes on the wintering of the timothy rust, *Puccinia Phleipratensis*, have been published by MERCER[7] and by HUNGERFORD.[8] MERCER states that in North Dakota it is difficult to find uredospores of this rust after the first hard frost, and that the fungus is not active until late July. The new pustules are on new growths in all cases, and therefore do not arise from hibernating mycelia, by means of which ERIKSSON and HENNING believe this rust lives through the winter in Sweden. Uredospores from rusted timothy straw exposed to the weather, but kept from moisture by means of open tin cylinders, did not germinate at any time from October to March.

In Wisconsin, HUNGERFORD finds that this rust behaves quite differently. Here uredospores capable of germinating were collected in the field in the months of October, November, December, January, and March. On plants that were taken up in March, sori developed on the new growth and also on flecked places on the old leaves. The latter undoubtedly arose from a hibernating mycelium.

MAINS[9] reports the wintering of *Coleosporium* (in Michigan?) by means of hibernating mycelia. Uredospores capable of germination were collected in February and May. On plants brought in during January, new pustules developed on the old rosette leaves.

The fact that the position of spore pustules of rusts, whether on the upper or the lower surface of infected leaves, is usually included in the diagnosis of

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[6] HECKE, L., Zur Frage der Überwinterung des Gelbrostes und das Zustandekommen von Rostjahren. Naturw. Zeitschr. Forst.- u. Landwirtsch. **13**:213–220. 1915.

[7] MERCER, W. H., Investigations of timothy rust in North Dakota during 1913. Phytopath. **4**:20–22. 1914.

[8] HUNGERFORD, C. W., Wintering of timothy rust in Wisconsin. Phytopath. **4**:337–338. 1914.

[9] MAINS, F. B., The wintering of *Coleosporium Solidaginis*. Phytopath. **6**:371–372. 1916.

species has led GREBELSKY[10] to undertake a study of this characteristic, in order to determine its constancy for given species and to discover the factors influencing the distribution of the sori. A statistical study of 42 species of rusts gave evidence that with few exceptions the uredinia are formed on the stomate-bearing side of the leaf. Especially striking illustrations are found in such forms as *Melampsora Larici-retusae*, which infects two species of willows, *Salix reticulata* with stomata only on the lower surfaces of the leaves, and *S. retusa* with amphigenous stomata. Here the distribution of the uredinia corresponds to that of the stomata, exceptions occurring only in leaves on which the infection is unusually severe. Some cases are noted, among them *Puccinia glumarum*, in which the sori do not occur on both sides of the leaves, although the stomata are amphigenous.

In a number of plants examined histologically it was found that the young sori always originate beneath the stomata; coating parts of the stomatal surfaces with wax led to the suppression of sori. By turning leaves with amphigenous stomata, but on which sori were normally produced on one side only, the author was able to shift the position of the sori to the other side of the leaves. Mere cultivation in the greenhouse induced sori normally present on one side of a leaf to become amphigenous. This result is attributed to the absence, on plants grown in the greenhouse, of wax coating by which the author believes the formation of sori is normally suppressed on the most heavily coated side of the leaf.

Some time ago, MORGENTHALER[11] showed that the production of teleutospores by rusts was determined by conditions internal to the host rather than by external factors. Further evidence of this relation has been brought out by GASSNER[12] in his studies of the South American grain rusts. The observations on *Puccinia triticina*, *P. coronifera*, *P. graminis*, and *P. Maydis* all indicate that teleutospore formation is associated with a definite state of maturity of the infected organ. Particularly clear and striking evidence that seasonal changes have little influence was obtained in the case of *P. triticina* and *P. coronifera*. On plants sown at intervals throughout the year, these rusts regularly produce uredospores followed by teleutospores. In *P. triticina* on wheat, production of teleutospores begins shortly before the appearance of the ear. This fact is particularly noticeable in varieties requiring different lengths of time for development. Seasonal influence is evident only in so far as it affects the development of the host. The teleutospores of *P. coronifera* on oats are also formed at the time of the appearance of the head, but with *P. graminis* on wheat, barley, and oats teleutospore formation does not begin

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[10] GREBELSKY, F., Die Stellung der Sporenlager der Uredineen und deren Wert als systematisches Merkmal. Centralb. Bakt. II. **43**:645–662. *figs. 12.* 1915.

[11] Rev. Bot. Gaz. **56**:162. 1913.

[12] GASSNER, G., Die Teleutosporenbildung der Getreiderostpilze und ihre Bedingungen. Zeitschr. Bot. **7**:65–120. 1915.

until the plants have reached a more advanced state of development. In general, the production of teleutospores appears to be associated with the depletion of the carbohydrates of the leaves. A direct influence of climatic or seasonal factors does not appear to exist.

DIETEL,[13] in the third instalment of his studies on the conditions affecting the germination of teleutospores, reports that the teleutospores of *Puccinia Malvacearum* germinate and form sporidia only in a saturated atmosphere. If the degree of saturation is only slightly below 100 per cent, normal germination does not take place. Furthermore, germination takes place only when water is abundantly supplied through the pedicels. When leaves of *Althea rosea* bearing rust sori were suspended in a saturated atmosphere in a bottle, but with the stems projecting into the air through the cork, no germination took place, although the leaves remained turgid. When the petioles were immersed in water, germination of the teleutospores in the sori began immediately. The author's interpretation of these observations is that the water necessary for germination is supplied to the teleutospores through the pedicels, but that an adequate supply is possible only under conditions of complete turgor of the host, and in a saturated atmosphere. The sporidia of *Puccinia Malvacearum*, it was noted, lose their vitality in one hour in an atmosphere of 90 per cent saturation, and in 10–16 hours even in a saturated atmosphere.

An unusual case of mycelial distribution is reported by FISCHER[14] for *Puccinia Dubyi*. The mycelium of micropuccinias is usually strictly localized, but in *P. Dubyi* FISCHER finds that the mycelium extends from the older infected leaves of the host (*Androsace*) through the stems to the newly formed whorls where new sori are produced. Instead of one crop of teleutospores usual in micropuccinias, this form produces a succession of sori through the season.

FROMME[15] reports that the germ tubes of the uredospores of *Puccinia Rhamni* are negatively geotropic, and that as a rule the germ tubes grow out from the pores on the non-illuminated side of the spore. Of 200 germ tubes issuing from spores illuminated on one side, 86 per cent had grown away from the light. The germ tubes of spores in darkness grew equally well in all directions. This property of the germ tubes undoubtedly is of significance in the process of infection.

Remarkable morphological changes in *Puccinia Ellisiana* and *P. Andropogonis* due to the influence of the host have been reported by LONG.[16] Both of

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[13] DIETEL, P., Versuche über die Keimungsbedingungen der Teleutosporen einiger Uredineen III. Centralb. Bakt. II. **42**:698–705. 1915.

[14] FISCHER, E., Beitrage zur Biologie der Uredineen. 6. Mycol. Centralb. **5**:113–119. 1914.

[15] FROMME, F. D., Negative heliotropism of urediniospore germ tubes. Amer. Jour. Bot. **2**:82–85. *figs. 2.* 1915.

[16] LONG, W. H., Influence of the host on the morphological characters of *Puccinia Ellisiana* and *P. Andropogonis*. Jour. Agric. Research **2**:303–319. 1914.

these rusts have their telial generations on species of *Andropogon*, and are distinguishable by evident morphological differences in their uredospores. *P. Ellisiana* has its aecidial generation on species of *Viola*, while the aecidial generation of *P. Andropogonis* occurs on species of *Pentstemon*. LONG now finds that *P. Ellisiana* will readily produce aecidia on *Pentstemon* also, but these aecidia resemble those of *P. Andropogonis*. More remarkable still is the fact that when plants of *Andropogon* are reinfected with aecidiospores of *P. Ellisiana* from *Pentstemon*, the resulting uredospores have all the characteristics of uredospores of *P. Andropogonis*. This rust can then not again be readily transferred to its original aecidial host, the violet. Conversely, *P. Andropogonis* can be made to infect species of *Viola*, but with great difficulty. If the aecidiospores thus obtained are sown on *Andropogon*, the resulting uredospores have all the characteristics of *P. Ellisiana*. In each case the morphological characteristics of the telial generation are determined by the aecidial host. From these facts the author concludes that *P. Ellisiana* and *P. Andropogonis* are but forms of one species. Since the transfer of *P. Ellisiana* to *Pentstemon* takes place readily, while the transfer of *P. Andropogonis* to *Viola* is accomplished with difficulty, he believes that in nature the transformation of *P. Ellisiana* to *P. Andropogonis* through the aecidial host, *Pentstemon*, is continually going on. The possible bearing of this discovery on the unexplained phenomena in the life histories of many rusts, and its consequent economic importance, are at once apparent.

Rust sori produced entirely within the tissue of the host do not seem to be of uncommon occurrence. To the number of known cases ADAMS[17] adds one of the occurrence of internal uredinia of *Uromyces Caryophyllinus* in the leaves of carnations, and COLLEY reports the finding of internal telia of *Cronartium ribicola* in the petioles of infected currant leaves. To COLLEY'S list of investigators who have reported internal sori of rusts should be added the names of BEAUVERIE,[18] who described internal sori in the seeds of grains and other grasses, and of REYNOLDS,[19] who mentions internal telia of *Puccinia Xanthii* in the leaves of *Xanthium canadense*.

In view of ARTHUR'S[20] recent revision of the rusts of the type of the orange rust on the blackberry in the United States, KUNKEL'S[21] paper, in which he clears up the anomalous situation created by his discovery[22] that the most

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[17] ADAMS, J. F., Internal uredinia. Mycologia **8**:181–182. *pl. 1.* 1916.

[18] BEAUVERIE, J., Les germes de Rouilles dans l'intérieur des semencis de gramineés. Rev. Gen. Bot. **25**:11–27. *figs. 10.* 1914.

[19] REYNOLDS, E. S., Relations of parasitic fungi to their host plants. BOT. GAZ. **53**:365–395. 1912 (p. 381).

[20] ARTHUR, J. C., Orange rusts of *Rubus*. BOT. GAZ. **68**:501–515. *fig. 1.* 1917.

[21] KUNKEL, L. O., Further studies of the orange rusts of *Rubus* in the United States. Bull. Torr. Bot. Club **43**:559–569. *fig. 1.* 1916.

[22] Rev. BOT. GAZ. **60**:80–81. 1915.

common orange rust of the blackberry is a short cycle form of the type of *Endophyllum*, needs merely to be mentioned here. The discovery of this rust, now known as *Kunkelia nitens* (Schwein.) Arthur, is a striking illustration of the proposition of TRANZSCHEL and of FISCHER, which may be generalized in the statement that the aecidial hosts of long cycle rusts often bear short cycle rusts whose teleutospores resemble one of the spore forms of the long cycle rust.

BARTHOLOMEW[23] finds that the mycelium producing the thin-walled spores which occur together or separately in the uredinia of the fern rust *Hyalopsora Polypodii* is binucleate throughout, and that there is therefore no reason for regarding the two spore forms as other than uredospores.

A very extensive investigation of the biological forms of *Puccinia graminis* in the area extending from the upper Mississippi valley through the northern great plains to the intermountain area of Washington and Idaho has been made by STAKMAN and PIEMEISEL.[24] Uredospores of *P. graminis* from about 30 species of grasses in this region were systematically sown on the common cereals and a number of other grasses, and in like manner uredospores from the cereals were sown on a large number of other grasses. The results of the many hundreds of cultures are tabulated in a readily comprehensible form. Six biological forms were isolated; of these, one, *P. graminis Tritici compacti*, is new. The others are the forms formerly distinguished, namely, *P. graminis Tritici*, *P. graminis Secalis*, *P. graminis Avenae*. *P. graminis Agrostis*. The extent of this work and the thoroughness with which it was carried out place the problem of the differentiation of biological races of *Puccinia graminis* in a much clearer light than has heretofore been accomplished. It is found that each biological form attacks a group of grasses not necessarily related. Within each group all degrees of susceptibility exist; the range from complete susceptibility to complete immunity is therefore gradual. The groups susceptible to the various biological races overlap considerably, so that the same grass may be host to a number of biological races of rust. Thus barley, rye, and *Bromus tectorum* have been infected by all of the 6 races of *P. graminis;* while oats has been infected by all except *P. graminis Tritici compacti*. The forms can nevertheless be differentiated by means of other grasses which are distinctly susceptible to some and immune to others of the biological races. These facts will probably explain the apparently different degrees of specialization of the forms of *P. graminis* by observers in different geographical regions. Within the region studied by the authors, no geographical specialization was observed. —H. HASSELBRING.

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[23] BARTHOLOMEW, E. T., Observations on the fern rust *Hyalopsora Polypodii*. Bull. Torr. Bot. Club **43**:195–199. *figs.* 3. 1913.

[24] STAKMAN, E. C., and PIEMEISEL, F. J., Biologic forms of *Puccinia graminis* on cereals and grasses. Jour. Agric. Research **10**:429–495. *pls.* 7. 1917.

Taxonomic notes.—BLAKE[25] has discussed the systematic position of *Clibadium* (Compositae), describing also 5 new species; has revised the genus *Dimerostemma* (Compositae), recognizing 6 species, 1 being new and 4 being new combinations; has described new Compositae (chiefly Mexican) under *Vernonia* (3), *Elephantopus*, *Ericameria*, *Erigeron*, *Conyza*, *Grypocarpha*, *Wedelia*, *Alvordia*, *Encelia*, *Simsia* (2), *Steiractinia*, *Pappobolus*, *Verbesina* (2), *Calea*, *Cacalia* (2), besides numerous new varieties, forms, and combinations; and also a new genus (*Rhysolepis*) based on *Viguiera morelensis* Greenm. The same author also describes new spermatophytes (chiefly from British Honduras), among them being a new genus of Apocynaceae (*Belandra*), and 52 new species distributed among 41 genera.

BUTTERS,[26] in the first of a series of taxonomic and geographic studies of North American ferns, has discussed the genus *Athyrium* as represented in various regions. In connection with the critical discussion of relationships, involving certain changes of nomenclature, 3 new varieties and several new forms are described under various species. The same author also presents the results of his studies of *Botrychium virginianum* and its American varieties, among which 4 are described as new.

BUTTERS and ST. JOHN[27] have described a new species of *Lathyrus* (*L. eucosmus*) from the Rocky Mountain region, and also two new varieties of *L. venosus*.

FERNALD[28] has published a fascicle of taxonomic notes, among which the following new species or varieties are described: a new variety of *Polygonum;* new varieties of *Ranunculus Purshii*, *R. pygmaeus*, and *R. reptans;* a new variety of *Anemone multifida;* a new species of *Saxifraga* and a new variety of *S. nivalis;* a new species of *Vitis;* and new varieties of *Cyperus filicinus* and *Aster cordifolius*.

HUTCHINSON[29] has published a revision of *Aspidopterys*, a genus of Malpighiaceae which includes a group of tall climbing shrubs of the forests of India and of the Malay Archipelago. He recognizes 22 species, 3 of which are described as new.

OSTERHOUT[30] has described a new *Mertensia* (*M. media*) from Colorado, closely related to *M. lateriflora* and *M. amoena*.

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[25] BLAKE, S. F., Contrib. Gray Herb. no. 52. pp. 106. 1917.

[26] BUTTERS, F. K., Contrib. Gray Herb. **19**:no. 51. pp. 169–216. *pl. 123. figs. 6.* 1917.

[27] BUTTERS, F. K., and ST. JOHN, H., Studies in certain North American species of *Lathyrus*. Rhodora **19**:156–163. 1917.

[28] FERNALD, M. L., Contrib. Gray Herb. New Series, no. 1. Rhodora **19**: 133–155. 1917.

[29] HUTCHINSON, J., Revision of *Aspidopterys*. Kew Bull. 1917:no. 3. pp. 91–103.

[30] OSTERHOUT, GEO. E., A new *Mertensia*. Torreya **17**:175, 176. 1917.

PITTIER[31] has published a revision of the Mexican and Central American species of *Lonchocarpus*, recognizing 40 species, 24 of which are described as new. He also describes 4 new species of the same genus from South America.

SMALL[32] has described a long known but unstudied tree cactus of the Florida Keys as a new species (*Cephalocereus Deeringii*). It had been "assumed to be identical with the species of *Cephalocereus* long known to grow on Key West."

SMITH,[33] in a first paper of a series of studies of *Lupinus*, describes a new species (*L. subvexus*) from California.

SWINGLE[34] has described a new genus (*Pamburus*) of Aurantiaceae related to *Citrus*. It is a native of India, and as yet includes only the type species *P. missionis*, which is *Limonia missionis* Wight. The same author[35] has also described *Pleiospermium* as another new genus related to *Citrus*, founded on *Limonia* Wight and Arn., and including two species.—J. M. C.

Embryo sac and embryo of Phaseolus.—Miss BROWN[36] has described the details of the development of the embryo sac and the embryo of *Phaseolus vulgaris*. The only previous study of this genus was by GUIGNARD in 1881, in his general work on Leguminosae, in which *P. multiflorus* is described. The details for *P. vulgaris* introduce no unusual situation, but it is valuable to know the facts in reference to so conspicuous a species.—J. M. C.

Fruit drop.—HODGSON[37] believes he has found a correlation between the June drop of the Washington navel orange and the daily fall in water content of the fruit and foliage. He says, "inasmuch as in the case of certain other plants the abscission of young fruits has been shown to be due to abnormal water relations, it is suggested that such may be the case here."—WM. CROCKER.

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[31] PITTIER, HENRY, The Middle American species of *Lonchocarpus*. Contrib. U.S. Nat. Herb. **20**:37–93. *pls. 6. figs. 43.* 1917.

[32] SMALL, JOHN K., The tree Cacti of the Florida Keys. Jour. N.Y. Bot. Gard. **18**:199–203. *pl. 206.* 1917.

[33] SMITH, CHARLES PIPER, Studies in the genus *Lupinus*. 1. A new species of the subgenus *Platycarpos*. Bull. Torr. Bot. Club **44**:405, 406. 1917.

[34] SWINGLE, WALTER T., *Pamburus*, a new genus related to *Citrus*, from India. Jour. Wash. Acad. Sci. **6**:335–338. 1916.

[35] ———, *Pleiospermium*, a new genus related to *Citrus*, from India, Ceylon, and Java. Jour. Wash. Acad. Sci. **6**:426–431. 1916.

[36] BROWN, MABEL MARY, The development of the embryo sac and of the embryo in *Phaseolus vulgaris*. Bull. Torr. Bot. Club **44**:535–544. *pls. 25, 26.* 1917.

[37] HODGSON, R. W., Some abnormal water relations in *Citrus* trees of the arid southwest and their possible significance. Univ. Calif. Publ. Agric. Science **3**:37–54. 1917.

VOLUME LXV NUMBER 5

THE
BOTANICAL GAZETTE

MAY 1918

MASS MUTATIONS AND TWIN HYBRIDS OF OENOTHERA GRANDIFLORA AIT.

HUGO DEVRIES

(WITH SIX FIGURES)

Under the name of mass mutation, BARTLETT has described a new phenomenon observed by him in *Oenothera pratincola* and *O. Reynoldsii*. Ordinarily, mutations occur in the species of *Oenothera* in about 1 per cent or less of the offspring of self-fertilized individuals, just as they do in the cases of *Linaria* and *Chrysanthemum* and in horticultural instances. In the species studied by BARTLETT (**1, 2**), about one-half or even a larger number of the offspring were seen to deviate from the parental type in a particular direction. These are called mass mutations; they may appear in the same sowings with normal mutations in other directions.

Oenothera pratincola has produced four mass mutants: mut. *formosa*, *albicans*, *revoluta*, and *setacea*; *O. Reynoldsii* two, mut. *semialta* and *debilis*. BARTLETT has pointed out that the phenomenon bears a certain degree of resemblance to Mendelian segregation, and assumes that the fundamental mutation possibly occurred in only one of the two gametes in a generation preceding the one in which the diversity becomes manifest (**2**).

Guided by these principles, I have studied the phenomenon of mass mutation in *Oenothera grandiflora* in connection with its ability to produce twin hybrids in certain crosses. This form of splitting in the first generation after a cross was first discovered

in *O. Lamarckiana* (**6, 9**), but was shown by DAVIS (**3**) to occur in *O. grandiflora* also. I found that *the twin hybrids may be considered as a consequence of the mass mutation*, the mutated gametes producing one of the twins and the typical sexual cells the other. This conception evidently may be applied to *O. Lamarckiana* and make some previous hypotheses superfluous,[1] but this point must be reserved for another article.

I shall first describe my cultures and crosses of *O. grandiflora* in a purely empirical way and afterward discuss their results in connection with those of BARTLETT.

A. MUTATIONS OF O. GRANDIFLORA

One of the last days of September 1912 I visited with BARTLETT a station of *O. grandiflora* in the neighborhood of Castleberry, Alabama. It was on the border of a cornfield situated along the railroad. The station seemed to us to be pure, since no other species of the same group could be discovered either in the field itself or in its neighborhood. The number of specimens was small, but had been very large some years ago, when the field was not cultivated. A few specimens bore ripe capsules, which we collected. From their seeds I started 10 pure strains. One of them was continued through four succeeding generations (1913–1916), whereas the others were abandoned as soon as they proved to contain in the main the same derivatives.

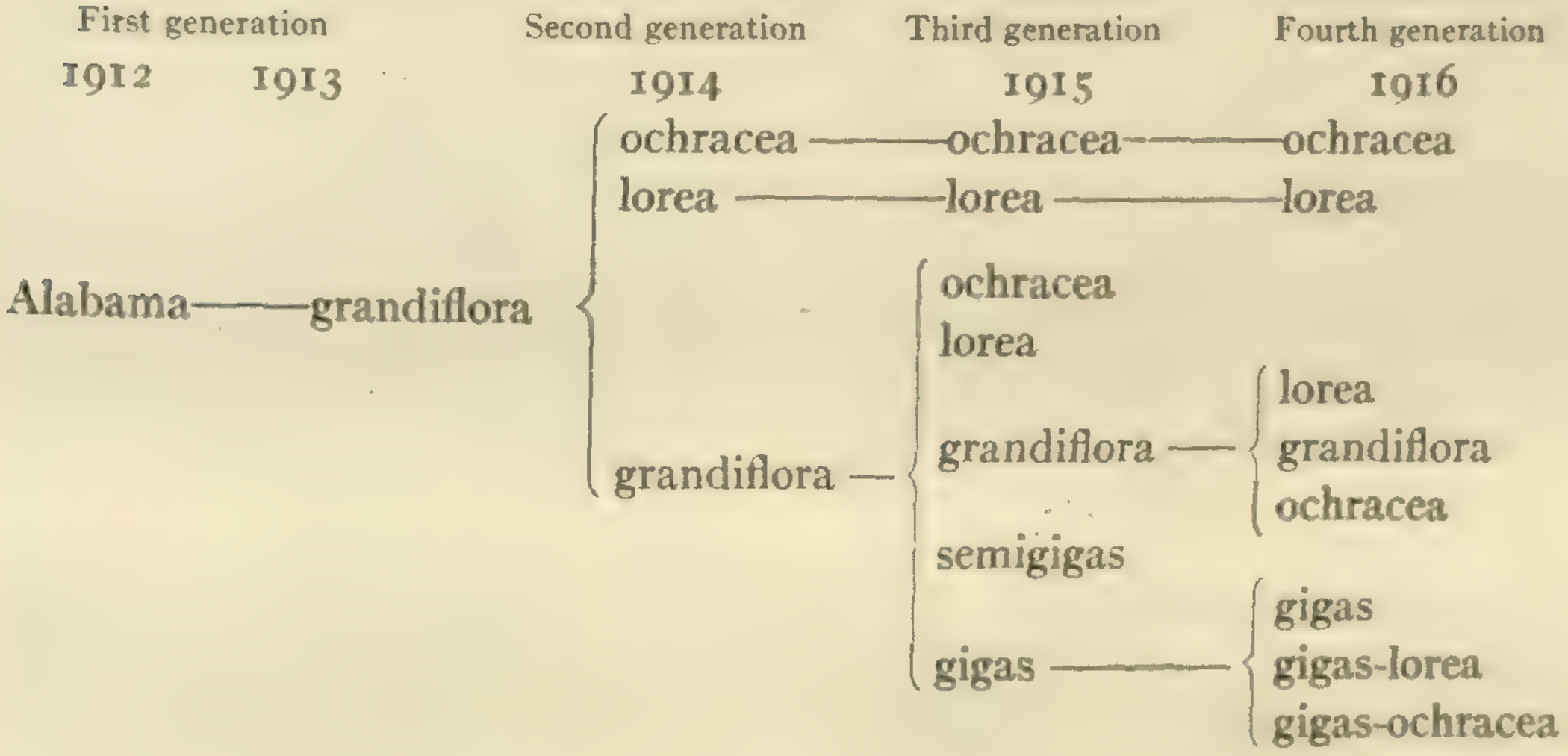
This race produced in my garden three mutations, two of which were observed in every generation, but the third was very rare, occurring only once.[2] All of them were constant in their progeny. I shall call them *ochracea*, characterized by broad and pale leaves, mostly weak and of a low stature (fig. 1); *lorea*, with almost linear leaves and somewhat narrower petals (fig. 2); and *gigas*, with stout stems, broad leaves and flower buds, large flowers, and 28 chromo-

[1] See *Gruppenweise Artbildung*. The conception of RENNER that the twins, and with them all mutability, might be the effect of a hypothetical hybrid condition of *O. Lamarckiana*, runs in some respects parallel to this view, but is contradicted by it on its main points. See Zeitschr. Ind. Abst. und Vererbungs. **16**: 279–284. 1916.

[2] All of the seeds for the different cultures were soaked in water under a pressure of 8 atmospheres during about 48 hours, and then sown at 30° C. in the greenhouse, so as to induce the most complete germination.

somes in its nuclei. As was to be expected, besides this *gigas* there was also found a *semigigas*, but since it was wholly sterile, little weight can be attached to it. GATES (10) observed a dwarf mutant of *O. grandiflora*, but no dwarf occurred among my cultures.

The pedigree of the whole culture is as follows. All fecundations were pure self-fertilizations, made by myself.



The numbers of specimens and the percentages of the splitting in this pedigree are shown in table I.

TABLE I

	Generation	Number of specimens	Percentage ochracea	Percentage lorea
grandiflora..	1	30	.....	.....
" ..	2	1476	(20)	2
" ..	3	1180	44	1
" ..	4	53	(15)	4
gigas.....	2	123	1	2.5
ochracea...	2	380	uniform	.....
" ...	3	58	"	.....
lorea.....	2	160	.....	uniform
"	3	61	.....	"

The control lines were derived from different specimens, grown in 1913 from the seed of Castleberry. They yielded the same two main mutants as given in table I. In the spring of 1914, however, before I discovered the presence of mutants, I had observed that a large number of the seedlings were very weak, dying off during the

first few weeks after being planted out in the boxes. Most, if not all, of these must have been *ochracea*, and the percentage of 20 for this mutant, found in August during the period of flowering, must have been far too small. For this reason it is put in parentheses, and the next year I tried to get a more reliable counting.

The seedlings of five self-fertilized plants of 1914 were planted out in boxes as carefully as possible, and before any essential loss

FIG. 1

FIG. 2

FIGS. 1, 2.—Fig. 1, *Oenothera grandiflora* Ait. from Castleberry, Alabama; and to right, *O. grandiflora* mut. *ochracea*, August 1915; fig. 2, *O. grandiflora* mut. *lorea*, August 1915.

was noted. They were kept in the greenhouse and counted out at the end of April. At that time some few were dead and decayed; others were dead but could still be judged. Since I had observed the boxes almost daily, it had been ascertained that it was always the pale ones which died, whereas the green seedlings grew without trouble. Thus I was confident that the dead had been *ochracea*, as well as the surviving pale ones. The number of the decayed was

derived from the number of specimens at the time of planting out, minus the number of survivals. The results of the count on April 25, 1915, are given in table II.

TABLE II

PARENT	TOTALS	GRANDIFLORA	OCHRACEA		LOREA
			Living	Dead	
No. 1.....	340	162	89	88	1
" 2.....	360	202	93	63	2
" 3.....	120	74	29	16	1
" 4.....	240	137	45	55	3
" 5.....	120	75	25	15	5
Total.....	1180	650	518		12
Percentage.....		55	44		1

The seedlings of the remaining five parents of 1914 were not counted in April, but at the time of flowering in August. Each of the groups yielded a large number of *ochracea* and one or more *lorea*, but the percentage for the first was now only 12. This figure is evidently due to the losses mentioned, since even during the summer usually many specimens of the type of *ochracea* are lost on account of their weakness. In 1916 I got about the same percentage at the time of flowering, but did not estimate the losses during the spring.

For this reason I repeated the sowing in the spring of 1917 with the preserved seeds of the same self-fertilized individual of 1915, taking every possible care to avoid the presumed losses. I planted out 70 seedlings, only one of which died; 20 were found in May to be *ochracea*, giving a total percentage of 30. This figure, therefore, should be substituted in table I for the 15 per cent given for the fourth generation.

Moreover, in 1917 I sowed the seeds of four other self-fertilized individuals of 1915, taking the same precautions. The culture embraced 224 seedlings, of which 8 per cent were pale and weak and died soon after being transplanted, while 31 per cent were recognized in May as *ochracea*. This gives a total of 39 per cent, which corresponds to the figures found in the best of the previous trials.

The percentages in April, as well as those found in August, show that the coefficient of mutation for *ochracea* is wholly different from that for *lorea* and from the ordinary coefficients for the mutability of *O. Lamarckiana*, *O. biennis*, and other species. The average of the three figures for *ochracea* given in table I is 26 per cent, and this figure is somewhat too low on account of the losses mentioned. It is evident, however, that it differs from normal coefficients of mutability in the same way as the mass mutations of BARTLETT, and that the production of mut. *ochracea* from *O. grandiflora* must be considered as another instance of this phenomenon. Here *the mass mutation is repeated in the succeeding generations of the pure line, and, in addition, mutations into lorea and gigas occur in the usual way.*

O. grandiflora mut. *ochracea*.—This species is well known as more strictly annual than any other of the same group. In spring it hardly makes any rosettes of radical leaves, but at once produces its stem. So did all my mutants, but especially the *ochracea* begins to make its stem when still very young and before being planted out. Its foliage is yellowish green, running parallel in this respect to *O. suaveolens* mut. *lutescens* (7). Even as in this last one, the leaves are strikingly broader and somewhat shorter than in the parent species. This insufficiency of the green color causes the young plants to stay behind the normal ones in their development, and by June they are much weaker. Afterward the new leaves assume a darker green, and in the fall the difference is often very small. The weakness remains, however, and the stature is low during the flowering period, reaching only 50 cm. in the beginning of July, when the normal plants are 70–80 cm. in height.

Most of the chlorophyll is developed along the veins. The teeth along the margin usually have red tips. The branches stand out from the stem at wide angles, sometimes almost horizontally. The spikes are loose, but the flowers are large and provided with a rich supply of good pollen; the fruits are cylindrical and often thin. These differences are small, apart from the color, but they are very constant. In fig. 1 they do not show so strikingly as they do on the beds. In consequence of the pale green color of the leaves the stems are thin and their wood is insufficiently developed; they are

often seen to decay, beginning in the lower part of the stem. Many specimens are lost from this cause during the summer.

As given in table I, I cultivated the *ochracea* through three succeeding generations, starting from the mutants of 1914. Two of them were self-fertilized; one yielded a progeny of 50 specimens, which constituted a uniform lot from the first beginning until the end of September. Among these I chose one of the strongest for self-fertilization, and had in 1916 from it a third generation of 58 plants, all resembling their parent. Most of them have flowered.

The other specimens of 1914 yielded seeds, some of which were sown in 1915 and some in 1916. In the first year I had 280 specimens, half of which flowered in August and September and were then pulled up, while the remainder flowered for the most part in October. They constituted a uniform lot of widely branched, low plants of pale green color. The culture of 1916 yielded 50 specimens, as pure and uniform as the former.

I crossed the mut. *ochracea* with the parent species in order to study its hereditary character. I made the crosses in 1915 and got the following progeny in 1916:

	grandiflora	ochracea	lorea	Sum
O. ochracea × grandiflora.....	41	18	1	60
O. grandiflora × ochracea.....	35	16	0	51
Total.....	76	34	1	111
Percentage.....	68	31	1	

The two reciprocal crosses gave evidently the same result, showing that both parents are isogamic in respect to their differential character. For this reason I repeated the sowing in 1917, transplanting the young seedlings after counting them, and determined the percentage of dying individuals besides that of the living *ochracea*. I found for two crosses of *O. ochracea × grandiflora* on May 12, 23 per cent dead seedlings and 35–27 per cent living *ochracea* in a total of 226; means 17 and 31 per cent, together 48 per cent. From the reciprocal cross I had only a small culture of 55 seedlings, among which, however, none died in early youth, while the percentage of the living *ochracea* was 40. The figure for *ochracea* is smaller than the highest one after self-fertilization

(44 per cent), but this obviously resulted from a loss of some pale individuals, which died off in early youth. The figure of 31 per cent was determined in June and should rather be compared with the percentages after self-fertilization determined at the flowering period (15–20 per cent). The *lorea* seedling was evidently due to a mutation, even as after self-fertilization.

O. grandiflora mut. *lorea*.—This mutant is characterized by its very narrow, almost linear foliage throughout its whole development. The leaves are dark green. The stature is almost the same as in the species, although at the end it is 2–3 dm. lower. Our climate, which is hardly favorable for the Alabama species, is still less so for this mutant. Not rarely the spikes miscarry, and bare anthers are of quite common occurrence. Especially in 1915 I found, during the whole summer, scarcely enough pollen for self-fertilization and some few crosses. The flowers are somewhat smaller and the petals less broad than in the parent species, and the fruits are thinner and more cylindrical. These differences are small, however, and probably a result of the insufficient nourishment by the narrow leaves. This latter character is always sharp and clear, and no intermediates have been observed. From two self-fertilized mutants of 1914 I cultivated a second generation, and from one of them I derived in 1916 the third one. They were uniform lots and strikingly different from the original species. They embraced in 1915 in the first instance 60 specimens, all of which flowered, and in the second about 100 seedlings, which were thrown away as soon as their uniformity was beyond doubt. The third generation in 1916 consisted of 61 plants, almost all of which flowered and resembled their parent.

I crossed *O. lorea* with *O. grandiflora* in 1915, but could not find pollen for the reciprocal cross. In June 1916 I had among 59 individuals 35 *grandiflora*, 15 *ochracea*, and 9 *lorea*, giving about 60, 25, and 15 per cent. The figure for *ochracea* is too low, since some seedlings were yellow and died in the seedpan, but it coincides sufficiently with the coefficient of mutation from the parent species as determined in the summer (15–20 per cent in table I). That for *lorea* is more reliable, since no losses could interfere here. It must be considered as due to the combination of all the mutated pollen

grains of *grandiflora* with *lorea* egg cells. It points to a high amount of mutated sexual cells, but my cultures were too small and too few to justify a further discussion of this interesting point.

I have also crossed the two mutants with one another. The results were as follows in June 1916:

	grandiflora	ochracea	lorea	Total
O. ochracea×lorea	22	8	0	30
O. lorea×ochracea	31	23	1	55
Total	53	31	1	85
Percentage	62	37	1	

The results of the reciprocal crosses may be assumed to mean the same hereditary conditions, even as in the crosses of the pale mutant with the species. The specimen of *lorea* seems to be due to a corresponding mutation in the *ochracea*, showing that this mutability is not as wholly absent here as the results of self-fertilization seemed to indicate.

In all these crosses the *lorea* marks must be assumed to be recessive to the *grandiflora* character. I have not made any second generations to decide this question, but the results of my crosses with allied species will fill up this gap and show that in crosses with *lorea* this type is split off, as a rule, in the second generation in proportions which correspond to the law of Mendel.

O. grandiflora mut. *gigas* (fig. 3) occurred in one specimen among the 1180 plants of my cultures of 1915, pointing to a coefficient of mutation of 0.1 per cent. This mutant attracted my attention in May and was planted separately with some other seemingly aberrant specimens. It opened its first flowers in the middle of August. They were strikingly larger, with broad, thick petals, a thicker tube of the calyx, thick filaments, anthers, and lobes of the stigma, and a rich supply of pollen. The flower buds were almost conical and the pollen was rich in quadrilateral grains, one of the characters of the *gigas* mutants of allied species. The nuclei of the young buds were investigated by my assistant Mr. C. VAN OVEREEM, who also counted the chromosomes in the young roots of the seedlings of the following year. The number was invariably 28, showing the

perfect analogy of this beautiful form with *O. Lamarckiana* mut. *gigas* and other giant mutants.

From the self-fertilized seeds of this mutant I had a bed of 123 plants in 1916. They were uniform, with the exception of some specimens of *lorea* and one *ochracea*. By May all of them had

FIG. 3

FIG. 4

FIGS. 3, 4.—Fig. 3, *O. grandiflora* mut. *gigas*, August 1915; flowering spike for comparison with fig. 1; *a*, opening flower bud of *O.* mut. *gigas; b*, flower of *O. grandiflora*, deprived of petals, for comparison with flower on spike of mut. *gigas; c*, opening flower bud of *O. grandiflora; d*, buds for next day's flowers of *O.* mut. *gigas; e*, same of *O.* mut. *grandiflora*; fig. 4, *O. biennis*×*O. grandiflora*, August 1915; to right *laeta;* to left *velutina*.

broader and thicker leaves than *O. grandiflora*, which was cultivated next to it for comparison under exactly the same conditions. The leaves of the young plants in June were 7 cm. broad, 20 cm. long, and a deep, downy green. In July the height was 60–70 cm., but the differences remained the same and very striking, the leaves of *O. grandiflora* being clearer green and only 4 cm. broad. The stems

were much stouter than in the species. During the flowering period the height of the plants exceeded that of the species only a little, but all organs were much stouter. The internodes were shorter and the number of leaves correspondingly larger. Over one-half of the whole culture have flowered, the remainder being pulled out earlier because unexpectedly the crowding of the plants became dangerous. It favors in this mutant, as in the species, the rotting of the stems.

In September I made the following measurements: height 2 m.; leaves of the upper part of the stem 5×15 cm. as compared with 3.5×12 cm., in *O. grandiflora;* petals 4.5 mm. as compared with 4.0×4.2 cm.; tube of calyx 4×50 mm. as compared with 2.5×35 mm.; flower buds 1.2×4 cm. as compared with 0.8×3.5 cm.; apex of petals with two deep incisions, which, in *O. grandiflora*, are often hardly perceptible; lobes of stigma and filaments of stamens much thicker than in the species. All these characters were very striking on the bed and made the culture one of the most showy of my garden, but the ramification was spare in the mutant; in the species it is ordinarily very rich.

The seeds of mut. *gigas* are about double the size of those of the species. I determined the amount of germs per hundred seeds for three self-fertilized specimens of my culture of 1916, and found 75–88 and 89 with an average of 84 per cent. This is only a little higher than the average for *O. grandiflora* itself, 75 per cent (4). In the roots of one of the three specimens mentioned the chromosomes had been counted by my assistant Mr. C. VAN OVEREEM; their number was 28, as in other instances.

It should be mentioned that the *lorea* and *ochracea* mutants from *gigas* had stout flower buds and large flowers like their sisters, and therefore must be considered as *O. grandiflora gigas lorea* and *O. grandiflora gigas ochracea.*

O. grandiflora mut. *semigigas.*—This mutant of 1915 differs the same way from the species as did the *gigas.* I did not find any striking difference between the two before the fruits ripened. They were stout in *gigas*, but small and thin in the other mutant, which for this reason could not be considered as true *gigas*, but evidently constituted only a *semigigas.* No fertile seeds could be obtained.

Since the occurrence of a mutant *gigas* gives full right to the expectation of mutants of the type *semigigas* with 21 chromosomes, I find no difficulty in the determination of the described specimen, but its value is only of a confirmatory nature.

B. TWIN HYBRIDS OF O. GRANDIFLORA

One of the most interesting peculiarities of *O. grandiflora* is the production of twin hybrids in certain crosses, analogous to the twins of *O. Lamarckiana*. This splitting was discovered by DAVIS (3) and since confirmed by my own experiments (4). The analogy is very close. All those species which split *O. Lamarckiana* into the twins *laeta* and *velutina* provoke the same phenomenon in *O. grandiflora*. Moreover, *O. biennis Chicago*, when used as a female parent in the crosses, splits both of them into *laxa* and *densa*. In their characters the twins of both species resemble each other so closely as to be easily identified, although it is evident that they cannot agree in all their characters. In those of *O. grandiflora* the differentiating marks are not so sharp as in the twins of *O. Lamarckiana*, and it is sometimes difficult to recognize them in the first culture which offers them. As soon as a second generation is grown, however, all doubts disappear.

The species which split *O. Lamarckiana* into *laeta* and *velutina* are *O. biennis*, *O. syrticola* (*muricata*), and *O. suaveolens* when used as female parents; *O. biennis Chicago*, when its pollen is used; and *O. Cockerelli* in both reciprocal crosses. *O. biennis Chicago* fecundated by *O. Lamarckiana* produces the twins *laxa* and *densa*. All these instances are duplicated by the analogous crosses of *O. grandiflora*. Moreover, *O. Hookeri* produces twins in the reciprocal crosses with *O. Lamarckiana* and also with *O. grandiflora*, but the results of these crosses are of a more complicated nature, and therefore will not be dealt with in this article. Table III gives a list of my crosses, together with their main results.

In *O. suaveolens*×*grandiflora* 18 per cent of yellow specimens appeared; in the other crosses, however, only the twins mentioned appeared. If we sum up the figures for *laeta* and *velutina* and take their mean, we find 52 per cent *laeta* and 46 per cent *velutina*, showing that the figures do not deviate essentially from equality for the

two groups. Mutants were rare in these cultures. Among the *laeta* of the first cross an *ochracea* and a *lorea* were seen, and among its *velutina* a *sulfurea*. Moreover, a *lorea* appeared in the second generation of the *laeta* of *O. lorea*×*Cockerelli*. The table proves the complete analogy between the splitting phenomena of *O. grandiflora* and *O. Lamarckiana*.

TABLE III

TWIN HYBRIDS OF *O. grandiflora*

CROSS	FIRST GENERATION		SECOND GENERATION	
	Percentage laeta	Percentage velutina	Percentage laeta	Percentage velutina
	A. laeta and *velutina*			
O. biennis×grandiflora	90	10	uniform	uniform
O. syrticola×grandiflora*	47	53	"	"
O. syrticola×grandiflora	42	58	"	"
O. suaveolens×grandiflora	61	21	.....	.....
O. Cockerelli×grandiflora	33	67	10 laeta 90 velutina	uniform
O. Cockerelli×grandiflora	28	72	.....	"
O. grandiflora×Cockerelli	52	48	83 laeta 17 velutina	"
O. lorea×Cockerelli	60	40	76 laeta 22 velutina	"
O. lorea×Cockerelli	40	57	.....	.....
O. grandiflora×Chicago	70	30	uniform	uniform
	B. densa and *laxa*			
	densa	laxa	densa	laxa
O. Chicago×grandiflora	83	17	uniform	uniform
O. Chicago×grandiflora	75	25	"	"

*The third generation continued uniform.

O. biennis×*grandiflora*.—I made this cross in 1914 and cultivated the first generation in 1915. It embraced 60 plants, almost all of which flowered in July and August. In the beginning of the flowering period I noticed the presence of two distinct types. The uppermost leaf beneath the spike was broad in *laeta* (3×10 cm.) and narrow in *velutina* (2×7 cm.), as were also the leaves and bracts. The color was yellowish and pale in the first, but less so in the

second type. The *velutina* began to flower about a week after the *laeta*. In August the height was 1.50–1.80 m., and the resemblance of the two types to *O.* (*biennis*×*Lamarckiana*) *laeta* and *velutina* was very striking, although the plants, as would be expected, were less stout. The flower buds of the *velutina* were thick, as usual, measuring 9×25 mm., as compared with 7×30 mm. for those of *laeta*. The free tips of the calyx were distant in the first, but pressed against one another in the second hybrid. The incision at the top of the petals was deep in the *velutina*, but slight in the *laeta*. The first were more hairy in all parts, especially on the flower buds and the younger parts of the axis of the spike. Their leaves were narrow, kennel-shaped, and smooth. The apex of the spike above the flowers was more densely covered by flower buds, but that of the *laeta* more loose, as shown in fig. 4. In all these respects the differences were the same as those between the twins of *O. biennis*×*Lamarckiana*.

I fertilized a *laeta* and a *velutina* and had in 1916 a progeny of 63 and 70 plants respectively, most of which flowered. The offspring of the *laeta* contained two mutants, an *ochracea* and a *lorea;* that of the *velutina* one, a *sulfurea*, with the same pale yellow petals as in *O. biennis* mut. *sulfurea*. Besides these, each of the cultures was uniform, resembling the parent in all respects. The differences were apparent in the boxes in May, at the time of planting out.

O. syrticola×*O. grandiflora*.—*O. syrticola* Bartlett is the *O. muricata* of my *Gruppenweise Artbildung*. I made two crosses in 1913, crossing each plant with the pollen of one individual of *O. grandiflora*, as usual. The figures for both cultures are given separately in table III; one of them was grown in 1914, but the other in 1915. From the first I had a second generation for each of the twins in 1915 and a third in 1916. They were uniform and resembled their parents. The size of these cultures was 4 and 49 for the *laeta*, but 61 and 70 for the *velutina*, which had given a better harvest. One mutant was observed among the *velutina* of 1915, having linear leaves and remaining very weak; apart from this the cultures were strikingly uniform, with the same differences as in the first generation and almost the same as those between the twins of *O. syrticola*×*Lamarckiana*.

In this first generation the differences were observed in the beginning of June, since the *velutina* were small plants with narrow kennel-shaped leaves, whereas the *laeta* were stout and had broad, flat leaves. These differences increased in July and August during the flowering period. The *laeta* were grass-green, but the *velutina* more gray; these latter had broad flower buds (7×22 mm. as compared with 5×27 mm. in the *laeta*). The petals were somewhat larger (3 cm.) in the *laeta* and smaller (2 cm.) in the *velutina*. The fruits were thin in the first named hybrid, but conical in the other.

O. suaveolens×*O. grandiflora*.—I made this cross in 1915 and cultivated only the first generation. It consisted of 61 per cent *laeta*, 21 per cent *velutina*, and 18 per cent of a third type, among 69 specimens, most of which have flowered. The three types were discerned in June and evident in July and August, although the differences between *laeta* and *velutina* were only small. Height of *laeta* in July 60–80 cm., of *velutina* 40–60 cm., midveins reddish in the first, white in the second. Leaves 3×10 cm. as compared with 3×15 cm. in July, and 3.5×11 cm. as compared with 2×9 cm. in August. The flower buds and flowers showed only small differences. The remaining 18 per cent were set off sharply against the rest, and this from the very beginning. They had the pale color, broad leaves, and low stature of the corresponding mutants of both parents, *O. suaveolens lutescens* and *O. grandiflora ochracea*. They must evidently be ascribed to the same mutability. Their flowers were intermediate between those of the parents. It should be noticed that this is the only case among all the experiments given in table III in which a third type showed itself besides the ordinary twins, apart from stray mutants.[3] This shows that a special feature of mutability in *O. suaveolens* must be responsible for it.

O. Cockerelli×*O. grandiflora*.—Since *O. Cockerelli* is an isogamic species, the results of both the reciprocal crosses are the same, with the exception that the hybrids of the cross just named are liable to be more or less pale in their foliage, as is so often the case in crosses in which *O. Cockerelli* is the female parent, as for example in *O. Cockerelli*×*suaveolens*. In our case it is the *laeta* which show

[3] Mutants of the *ochracea* type were seen among the *laeta* of the second generation from *O. grandiflora*×*Chicago;* see later.

this insufficient development of the chlorophyll, whereas the *velutina* is dark green. The main interest of these crosses lies in the fact that their *laeta* do not give a uniform progeny, but split into *laeta* and *velutina*, exactly as in the case of the hybrids of *O. Hookeri* and *O. Lamarckiana* (5). The *velutina* constitute constant races in both instances.

I made the cross *O. Cockerelli*×*O. grandiflora* twice, once in 1914 and once in 1915. They yielded 58 and 64 offspring, among which 33 and 28 per cent were *laeta* and 67 and 72 per cent *velutina*. These twins resembled those of *O. Cockerelli*×*O. Lamarckiana*, but some of the *laeta* had a yellowish green foliage and were more or less weak in constitution for that reason. The *laeta* had broad leaves (4.5×15 cm.), whereas those of the *velutina* were narrow (3×15 cm.), and the same difference prevailed between the bracts of the spike. This character was very conspicuous on the beds, especially when compared with the cultures of the next generation. Moreover, I had a lot of *O. syrticola*×*O. grandiflora* at the same time and found the types of both twins to be essentially the same as in this cross.

In the second generation the *velutina* were uniform and repeated the characters of the parent. The culture embraced 70 flowering plants. They were a strikingly uniform lot, and made the distinction of the two types in the first generation as well as among the progeny of the *laeta* quite easy. These latter consisted also of 70 flowering specimens, which were counted in July, shortly before the opening of the first flowers. They gave the percentages shown in table III.

O. grandiflora×*O. Cockerelli*.—Apart from the fact that all the hybrids are of a normal green color, this cross simply repeats the reciprocal one. I crossed two specimens in 1914 and had the first generation of 80 individuals in 1915. They showed in July 52 per cent *laeta* and 48 per cent *velutina*, with the same differences as previously given and the same resemblance to the twins of *O. syrticola* ×*grandiflora*. About one-half of the plants flowered, the flower buds of the *laeta* being relatively thin, but those of the *velutina* thick (5×20 mm.) and hairy. The second generation gave a uniform lot of 70 flowering plants for the *velutina* and a dimorphic

culture for the *laeta*. In this the types were exactly the same as in the previous year. There were 57 *laeta* and 12 *velutina*, as counted in July, when the differences were most sharp.

O. grandiflora lorea×*O. Cockerelli*.—Apart from the appearance of a few individuals of the *lorea* type, this cross gives the same result as the analogous cross of the species itself, and the hybrids are just the same, not showing the least influence of the almost linear leaves of the mutant mother. I made the cross twice, in 1914 and 1915. The first one gave 80 specimens with 60 per cent *laeta* and 40 per cent *velutina*, but without *lorea*. The second gave 81 flowering plants, among which 23 were *laeta* and 58 *velutina*. Two weak specimens had the leaves of *O. grandiflora lorea*. If we wish to explain their occurrence we must, perhaps, take into consideration that in culture of hybrids of *O. Cockerelli* with other species weak specimens with linear leaves are seen from time to time. In the second generation I expected to find some specimens of *lorea*, but only one appeared among the *laeta*. The culture embraced 64 plants, with 49 *laeta* and 14 *velutina*. I also derived a second generation from the *velutina* of the first; it had the same number of specimens, all of which flowered, but they were wholly uniform and like those just described.

O. grandiflora×*O. biennis Chicago* (cross of 1913).—First generation in 1915 with 40 flowering specimens, among which 12 were weaker than the others from the very beginning, and proved in August, when they flowered, to belong to the type of *velutina*, having narrower leaves. There were still some doubts concerning this identification, but they disappeared when the second generations were cultivated in 1916. These embraced the offspring of two specimens of *laeta*, each consisting of 70 flowering plants, and that of two *velutina*, with 47 and 60 specimens.

The differences were evident by May, since the leaves were broad and clear green in the *laeta*, but narrower and darker in the *velutina*. The *velutina* were quite uniform, but among both groups of *laeta* some specimens showed the broad leaves, pale color, and low stature of the mut. *ochracea* (7 and 12 specimens). The two main types were both intermediate between their parents and much resembled the corresponding twins of *O. Lamarckiana*×*Chicago*.

Leaves of the stem of *laeta* were pale green and broad (4×14 cm.); those of *velutina* dark green and narrow (2.5×12 cm.). Flower buds were shorter and thicker in *velutina* than in *laeta*. The flowers themselves and the fruits were alike in the two twins.

O. biennis Chicago×*O. grandiflora* gives twins which resemble those of *O. biennis Chicago*×*O. Lamarckiana* so closely that there can be no hesitation in identifying them. I made the cross in 1913 on two specimens of the female parent, fertilizing them each with the pollen of one *grandiflora*, but cultivated one offspring in 1914 and 1915, the other in 1915 and 1916, so that in 1915 I had a first and a second generation on the same bed. The results were sensibly the same, as may be seen in table III. The leaves of the *densa* were clearly broader than those of the *laxa*, especially in July and August, when they flowered. In the *densa* the foliage was more dense and the plants more richly branched but lower of stature, and more like the female parent of the cross. The size of my cultures was 70 and 40, mostly flowering plants in the first generations, 60 for each of the second generations of *laxa*, and 70 for each of those of *densa*, making together 370 specimens. The differentiating characters of the first generation were repeated in the uniform lots of the second, where they proved to be clear and sharp.

O. grandiflora ochracea×*O. Cockerelli*.—Since the mass mutant *ochracea* behaves differently from mut. *lorea* in so many respects, I have studied its behavior in this cross and the reciprocal one, in order to see whether the splitting into *laeta* and *velutina* would be repeated or not. I did not find it. Both crosses were made in 1915. In 1916 their progeny embraced 60 and 37 specimens. This latter number was small, because this reciprocal cross produced numerous yellow seedlings, most of which were pale green and did not succeed in developing their first leaves. Only 43 survived in the seedpan, and among these 6 proved still too weak for a normal growth. It is the same phenomenon often seen among the hybrids of *O. Cockerelli* with other pollen. The culture retained some degree of paleness during almost the whole summer. Apart from this, the hybrids of the two reciprocal crosses were the same and constituted one uniform lot. In June the absence of *velutina* was clear; the

hybrids of *ochracea*×*Cockerelli* had broad leaves (6–7 cm.) and were stout green plants, whereas those of the reciprocal cross were still pale. I compared them with the hybrids of *O. grandiflora*× *Cockerelli* and with those of *O. grandiflora lorea*×*Cockerelli* which grew quite near to them. In the beginning of August they began to flower and almost all of the plants of both cultures reached this phase before the end of the month, reaching a height of 1.50 m. They were uniform groups and in all respects like the *laeta* of the corresponding crosses, with the exception of the paleness of one of the two sets; but this diminished gradually as the summer advanced. The leaves and bracts of the inflorescence were still very broad and flat. There were no specimens like the *velutina* of the crosses with *O. grandiflora* and *O. lorea*.

C. UNIFORM HYBRIDS

O. grandiflora×*O. syrticola*.—The hybrids derived from the pollen of *O. syrticola* (*O. muricata*) have often the type described as *gracilis* in my *Gruppenweise Artbildung*. This is especially the case with those of *O. Lamarckiana*, and the hybrids to be described here simply duplicate these latter. I made the cross twice, in 1913 and 1914, and had the first generations of 80 and 30 plants in 1914 and 1915. From the latter I derived a second generation from two self-fertilized individuals of the first. They were uniform lots when they flowered, embracing 7 and 44 specimens with the slender stature and characteristic foliage and stature of *gracilis*, but many seedlings had been yellow and died before making their leaves, exactly as in the first generation. In this the uniformity of the type was already evident in the beginning of June, before the full development of the stems, by the brownish color of the stems and foliage and the narrow, almost linear, leaves. The resemblance to *O. biennis*×*syrticola* increased during the growth of the stems and the development of the spikes. At the time of flowering the plants measured only 80–120 cm.; their top was curved sideward as in *O. syrticola*; the flowers were small and 3–5 of them opened every evening; lobes of the stigma short and thick; leaves narrow, slightly kennel-shaped, and bluish green. It is easily seen that the characters of the father prevailed in the hybrid.

O. grandiflora×*O. biennis*.—This combination corresponds to the cross *O. Lamarckiana*×*biennis*, which gives uniform hybrids of a type in which the characters of the male parent largely dominate; but the results are very different, as we shall presently see.

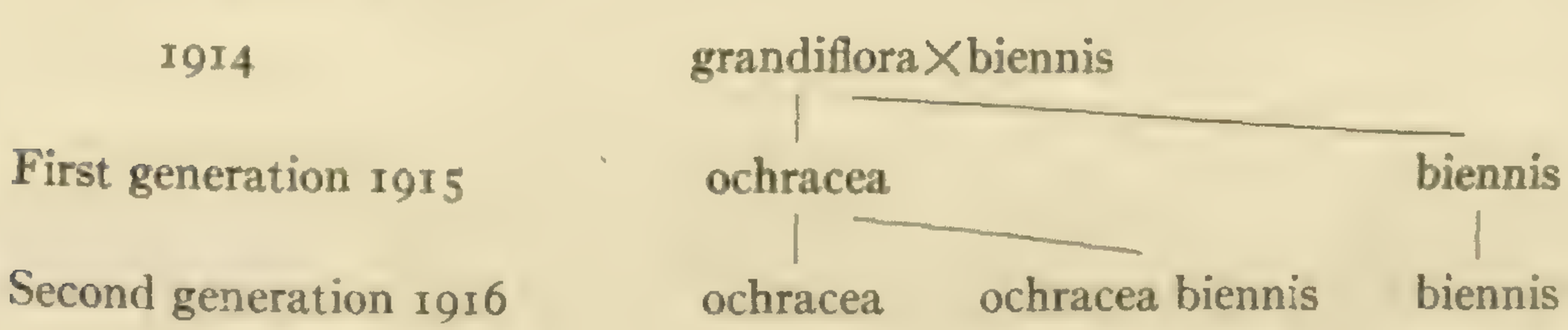
The two parents of the cross have both a large supply of good seeds. The character of *O. Lamarckiana* to produce at least one-half of empty grains is not present in either of them. There is no reason to expect this phenomenon among their crossed seeds, therefore, and as a matter of fact I counted 85 good germs in 100 seeds from this cross; whereas the reciprocal cross, which produces the *laeta* and *velutina* as we have seen, had 79 germs in 100 seeds. The figures do not essentially differ.[4]

I made the cross in 1914, and in 1915 had a set of 54 plants, among which 45, or 83 per cent, resembled their pollen parent in almost all respects, whereas 9, or 17 per cent, repeated the marks described for the mut. *ochracea*. All of the latter and the larger part of the former flowered in August. In the *biennis* type the leaves were narrower (3.0×11 cm.), with reddish midveins; whereas the *ochracea* had the ordinary broad leaves (3.5×11 cm.) and white veins. The stature of the *biennis* exceeded that of the *ochracea* in July by 10–20 cm. (60 cm. as compared with 40–50 cm.). During August these differences gradually increased and the spikes with ripening fruits were compact in the one and loose in the other type, corresponding to those of the pollen parent and of the mutant. The hybrids of the *biennis* type became at the end very stout, reaching almost twice the height of the *ochracea* plants. In 1916 I cultivated a second generation from each of the two types, embracing 70 and 51 specimens, most of which flowered. The offspring of the *biennis* plants were a uniform lot, exactly repeating the characters of their parent; those of the *ochracea* were dimorphic. Some plants made first a rosette of large radical leaves and from this produced a stout stem, whereas the others did not produce a rosette, but at once grew up, causing the stems to be thin and weak. It should be mentioned that the initial rosettes are a character of *biennis*, whereas

[4] My determinations gave, as a mean from 7 countings of lots of 200 seeds each, 75–76 per cent of seeds with normal germs for the cross *O. Lamarckiana*×*biennis* (see 4, p. 268).

O. grandiflora normally produces stems without this preliminary step. In the first generation the differences had been the same in this respect, the *biennis* plants having preparatory rosettes and stout stems, but the *ochracea* lacking these characters. Thus we see that this mark returned in part of the specimens of the second generation. I shall simply call the plants growing up without rosettes *ochracea*, and retain for the others the term "*biennis*,"[5] but both types had the broad, yellowish leaves of the *ochracea* of the first generation, and its loose spikes. I counted in August 33 per cent of the *biennis* and 67 per cent of the *ochracea* type.

Resuming these descriptions we see that the second generation of the first *ochracea* hybrids was constant and like the parent in all respects except the rosette character. This was absent in two-thirds of the specimens, which thereby were just like their parents, but present in one-third, which returned to the mode of growth of the other grandparent. This disposition may be expressed by the following pedigree:



This pedigree shows the splitting of the *biennis* character in the first and second generations and the constancy of the *ochracea* marks in the second. For the majority of the marks of *ochracea* it runs parallel to the ordinary scheme for the splitting into *laeta* and *velutina*, but for the character of the rosettes it is parallel to that of the *laeta* and *velutina* produced by the crosses between *O. Hookeri* and *O. Lamarckiana*, where the *laeta* is known to split off *velutina* in the succeeding generations. The explanation which offers itself is that the annual growth is here dominant over the

[5] I would have preferred to call them annual and biennial, since one group assumes the annual habit of *O. grandiflora* and the other the biennial growth of *O. biennis* L.; but as I cultivated all of them as annuals, it does not seem advisable to use these terms here. The chosen terms relate obviously to one prominent character; they should not convey the conception that all other characters are the same as in the prototypes of the names.

initial rosettes. These are recessive in part of the first generation, but return in their offspring in one-third of the specimens, in about the same way as in the corresponding formula of Mendel. I have not tried to go deeper into these questions, however, which touch the mutability of *O. grandiflora* only slightly, but have limited myself to two further experiments.

O. grandiflora ochracea × *biennis*.—The results of this cross have been the same as in the pedigree just given, with the exception that the splitting in the first generation fails. The cross was made in 1914, and the culture of 1915 was a uniform set of 70 plants, most of which were very weak and died off before flowering. Only 15 reached this stage. They grew up like the normal mutant *ochracea* and had from the beginning its slender stems, broad and pale leaves. No specimens of the type of *biennis* were seen. After self-fertilization a splitting occurred. Some plants were green and stout; the majority, however, were pale and weak. All of them had the broad leaves of *ochracea*, but 9 among 80 made vigorous initial rosettes, whereas the remainder grew up without this preparation. This gives a percentage of 89 *ochracea* and 11 *biennis*. The description for both types is the same as in the cross between the two species.

O. grandiflora lorea × *biennis*.—The narrow leaves of mut. *lorea* are recessive to the broad form of the leaves of the species. In other respects the mutant does not seem to differ from it, and thus I could expect this cross to give almost the same results as the first. I began the experiment in 1914, and in 1915 had the first generation with 60 plants, most of which flowered. I counted 9 *ochracea* without rosettes, or 15 per cent; the others were of the biennial type. Both types agreed in all respects with those of the cross between the pure species.

The second generation from the *biennis* plants was uniform, repeating the type of the parent. I had 70 plants, half of which flowered. They were very stout, and already so in the phase of rosettes. When flowering, the bed looked almost like pure *O. biennis* L. No *ochracea* and no *lorea* were seen among them.

The seeds of self-fertilized specimens of *ochracea* of the first generation produced in 1916, among 67 plants, a very striking splitting

into two types, 57 per cent being stout plants like *biennis* and reaching 1.5 m. in height when they flowered. The others lacked the initial rosettes but were not *ochracea*, evidently being *lorea* with the narrow, dark green leaves of this type. They were far less stout and reached only 1.20 m. in height and flowered some weeks later than the *biennis*. The mut. *lorea* grows always without a preparatory rosette and resembles in this respect the *O. grandiflora*. From this we may conclude that the splitting in our pedigree was exactly the same as that between the two species, with the exception that the *lorea* marks hid those of *ochracea* in the second generation.

I will now resume the results of the three crosses made with the pollen of *O. biennis* L.

TABLE IV

CROSSES OF *O. grandiflora* AND *O. biennis*, MADE IN 1914

Cross	First generation		Second generation from ochracea		Second generation from biennis
	Percentage ochracea	Percentage biennis	Percentage ochracea and lorea	Percentage biennis	
O. grandiflora × biennis	17	83	67 ochracea	33	uniform
O. grandiflora lorea × biennis	15	85	43 lorea	57	"
O. grandiflora ochracea × biennis	uniform	.....	89 ochracea	11	.....

If we assume that in *O. grandiflora* the mass mutation into *ochracea* takes place at the time of synapsis, and that the egg cells are therefore mutated before fecundation, we may deduce from table IV that normal egg cells of the species, after fecundation by *O. biennis* L., give uniform hybrids of the *biennis* type, whereas the mutated egg cells reproduce the type of *ochracea*. This would explain the dimorphous condition, where uniformity would otherwise be expected.

O. grandiflora × *O. suaveolens*.—I made this cross on two specimens in 1915, but got a very small harvest of seeds, yielding only 8 and 13 seedlings. In June the same two types were seen as in the cross of *O. grandiflora* × *biennis*. I counted 2 and 4 *ochracea*

with broad leaves, a low stature, and weak constitution, and with stems without preparatory rosettes. Among the remaining plants 6 and 8 were intermediate between the two parents, with stout, sparely branched stems and dark green leaves of an intermediate form. Besides these there was one *lorea*. All of these plants flowered in August, and showed in their flowers intermediate characters; but I have not continued the experiment.

D. FIRST GENERATION OF CROSSES WITH LAMARCKIANA

Both *O. grandiflora* and *O. Lamarckiana* produce twin hybrids in a number of crosses. If they are fertilized among themselves, therefore, combinations of these twins may be expected. Moreover, it is known that from crossed seeds and from seeds of hybrids the same mutations may arise as from the parent species. In this way I observed two hybrids with the characters of *gigas*, some with those of the dwarfs, and a third type of doubtful relations. These mutants are rare, however, whereas the products of the splitting were observed in all my experiments.

For my crosses I have not only used the two species themselves, but also one of the mutants of each of them, *O. Lamarckiana nanella* and *O. grandiflora lorea*. Their special characters were latent in the first generation, and the results of their crosses were identical with those of the species. They simply give a confirmation of the main result. This consisted in the appearance of three types, which it seems desirable to distinguish by special names. I shall call these triple hybrids *ovata*, *lutea*, and *brunnea*, in connection with their most striking features. The mutant previously mentioned, for which I have not succeeded in studying the identity with one of the mutants of the parents, I shall call, for convenience, *contraria*. It seems destined to play only a subordinate rôle in the discussion concerning the splitting which produces the triple hybrids.

O. hybr. *ovata* is seen almost always in the largest numbers. It is stout and richly branched, with broad leaves of pure green and dense spikes of large flowers. In spring it makes a large rosette, like those of *O. Lamarckiana*, and from its center produces a vigorous stem in June. The foliage is that of *O. grandiflora*, and the leaves in the middle part of the stem are hairy, show some bubbles,

and measure approximately 4×17 cm. The combination of this foliage with the thick stems and branches of *O. Lamarckiana* constitutes the most striking mark; the hybrid is obviously intermediate between its parents. The flower buds resemble those of *Lamarckiana* and have a tinge of brown, which is subjected to some amount of fluctuating variability. The flowers are large and the

FIG. 5

FIG. 6

FIGS. 5, 6.—Fig. 5, *O. grandiflora*×*O. Lamarckiana* mut. *nanella:* branches of triple hybrids shortly before flowering; *O. ovata* (about 50 per cent); *L. lutea*, and *B. brunnea* (each about 25 per cent of offspring); fig. 6, *O. grandiflora*×*O. Lamarckiana* mut. *nanella:* flowering spikes (deprived of flowers just open), showing characteristic position of flower buds; to left, *O.* hybr. *lutea;* to right, *O.* hybr. *ovata*.

petals cover one another by the margins, but this mark is also variable, and sometimes the petals are seen to have a wedge-shaped base. The fruits are stout and of an intermediate form.

O. hybr. *lutea* differs little from *ovata* in form, but its color is strikingly yellowish instead of pure green. This is seen in the foliage and very evident in the flower buds, but may disappear when the season advances. The leaves are almost as large. I measured

strictly comparable instances for comparison with the figures just given and found 4.5×14 cm., that is, a little broader and shorter than *ovata*. The spike is destitute of red color, or almost so, in all its parts, and this is often the most striking mark. The flower buds are pale and stand off at wide angles from the axis. The flowers are large and the petals have usually a broad base, as in *O. Lamarckiana*. The stems are not as stout nor as richly branched as in *ovata*, but this is probably due to the less amount of chlorophyll. The fruits are like those of the other type.

O. hybr. *brunnea* is a very striking form, especially when cultivated in large numbers of the second generation, which is uniform. It is as high as *ovata*, but less stout; its branches are more erect, its flowers and fruits erect and almost pressed against the stem. The leaves are smooth and narrow, measuring approximately 1.5×8.5 cm. (as compared with 4×17 and 4.5×14 in the two others) and the stem and foliage are brownish, contrasting sharply with the two other types. Even in early youth the differences are sharp enough, although some individuals may remain doubtful, especially when the space at their disposition is not sufficient, but the flowering spikes make all doubts disappear.

O. hybr. mut. *contraria* resembles the *brunnea*, but has larger leaves, measuring approximately 2.5×10 cm., and the color is less brown. The flower buds are thinner and yellowish. It looks like a different combination of the marks of the triple hybrids. Perhaps it is related to *O. Lamarckiana* mut. *oblonga*.

O. hybr. mut. *gigas*.—This occurred in the first generation of a cross between *O. lorea* and *O. Lamarckiana*, and in another between *O. grandiflora* and *O. nanella*. Both were recognized by their broad flower buds, resembling those of *O. Lamarckiana gigas*. The first was a stout plant 1.5 m. high, but little branched, with broad and thick leaves, a short and thick calyx tube, and short and thick fruits. In its other marks it belonged to the type *ovata*. Its pollen consisted almost entirely of quadrangular grains, which were almost completely fertile. Moreover, it was fertile after self-fertilization. Its seeds contained 89 germs in 100 grains. Evidently it was a *gigas* and not a *semigigas*. The other mutant was a *lutea* with thick flower buds. It produced with its own pollen only one fertile

seed, which germinated in 1916. Unfortunately this seedling was attacked by some disease, but it flowered in September with the buds, flowers, and pollen of a pure *gigas*, and showed 28 chromosomes in the nuclei of its roots in preparations made for me by my assistant Mr. C. VAN OVEREEM.

O. hybr. mut. *nanella* were dwarfs like the hybrid dwarfs of *O. Lamarckiana*. They appeared in the second generation of *lutea* specimens from crosses between *O. Lamarckiana*×*lorea* and *O. lorea*×*nanella*.

I made my crosses in different years and cultivated about 30 or 60 offspring of each. I counted them in July at the beginning of the flowering period, when the characters were most sharp and no doubtful specimens remained. I made one cross first in 1913, and the others in the two following years, so as to have cultures of the second generation along with the trials of the first. This, of course, is the best means of thoroughly comparing the types during the tests.

The size of the cultures is too small to give reliable proportions for each of them. Their aim is to show that the three types arise from every combination without exception, and that the mutants arise only occasionally. The size of the whole group, however, is large enough to warrant the reliability of the average proportions. In calculating these I have reckoned the *gigas* plants with the *ovata* and the *lutea* respectively, on the ground of their general appearance. The *contraria* were calculated separately. No other types occurred, especially no *lorea*, no *ochracea*, no dwarfs, and none of the special types afforded by later generations.

Some details may be given now concerning these experiments.

O. grandiflora×*O. Lamarckiana*.—Cross of 1914 between two specimens of my races. I cultivated 60 offspring until July, but retained only one-half of them during August and Septembér. This half had been planted on a bed in April, before the distinguishing marks were clear. In July I counted 30 *ovata*, 11 *lutea*, and 18 *brunnea*, but could not distinguish the *contraria*. For this reason only the results of the counting on the bed in August have been given in table V. The three types were exactly the same as in the other cultures. Of each of them one plant has been fertilized in order to study their second generations in 1916.

O. grandiflora lorea×*Lamarckiana* (cross of 1914).—In July I had on the bed 10 *ovata*, 12 *lutea*, 8 *brunnea*, and 3 doubtful ones, and in the box 25 *ovata*, 9 *lutea*, and 6 *brunnea*. All of the first and the larger part of the second culture were annual. I retained only those on the bed and controlled their numbers during August, when they flowered, and then found that the doubtful specimens belonged to the type of *contraria*. One specimen of each type has been fertilized and has yielded a second generation in 1916.

TABLE V

O. grandiflora×*O. Lamarckiana* AND DERIVATIVES; FIRST GENERATION

Cross	Year of culture	Triple hybrids			Mutants		Total
		ovata	lutea	brunnea	contraria	gigas	
O. grandiflora×Lamarckiana	1915	12	7	8	3	0	30
O. grandiflora lorea×Lamarckiana	1915	10	12	8	3	0	33
O. grandiflora lorea×Lamarckiana	1916	29	13	17	0	1	60
O. Lamarckiana×grandiflora	1915	22	3	5	0	0	30
O. Lamarckiana×grandiflora lorea	1915	21	4	5	0	0	30
O. grandiflora×nanella	1914	35	12	7	0	0	54
O. grandiflora×nanella	1915	11	2	6	9	1	29
O. grandiflora lorea×nanella	1915	23	2	5	0	0	30
O. grandiflora lorea×nanella	1916	22	25	13	0	0	60
Total		185	80	74	15	2	356
Percentage		52	23	21	4		

A second cross was made in 1915, with the second generation of *lorea*. The culture embraced 60 plants, almost all of which flowered, and which could easily be counted in August. No *contraria* was observed during the period of flowering, but a mutant *gigas* appeared, as has been described. I repeated the counting of this group at different periods, in order to be sure that the same figures were obtained. The plants reached a height of 1.5 m. about the middle of August.

O. Lamarckiana×*grandiflora* (cross of 1913).—Seeds sown in 1915, after a first trial in 1914. Besides the plants mentioned in the table, I had another set, which contained some *brunnea* but no *lutea;* it was thrown away in July. The plants on the bed flowered in August.

O. Lamarckiana×*grandiflora lorea.*—Culture of 61 plants, of which only one-half had been planted out on the bed and flowered in August. The other half consisted in July of 22 *ovata*, 4 *lutea*, and 5 *brunnea*, giving almost exactly the same proportions as those on the bed.

O. grandiflora×*O. Lamarckiana nanella.*—For this and the next crosses the dwarfs of the same race were used, as for almost all my previous crosses with dwarfs. I made the cross on two specimens of *grandiflora* in 1913 and sowed the seeds of one of them in 1914 and of the other in 1915. The first culture showed no *contraria;* the second, however, was extraordinarily rich in them. It contained, moreover, the *lutea* specimen with the flowers of a *gigas*.

The group of 1914 was the first of all my cultures to show the splitting. Before June only two types were distinguished, the yellow plants being considered as weak specimens of the main type. About the middle of June, however, they proved to have broader leaves and quite different flower buds, and were considered to constitute a new type. The final proof of this conception was only reached in 1915, when I cultivated the second generation of the three types, and could observe their distinguishing marks on large sets of plants. In 1914 I counted one-half in the box, and the other at different times on the bed; the sum of the two groups is given in the table.

The culture of 1915 confirmed that of 1914, apart from its mutants. I counted 11 *ovata*, 2 *lutea*, and 6 *brunnea* on the bed, besides 17, 5, and 8 of the same types in the box. These latter have not flowered, however, and for this reason are omitted in the table.

O. grandiflora lorea×*O. Lamarckiana nanella.*—I crossed a mutant *lorea* in 1914 and a specimen of the second generation in 1915. The first cross gave, besides the flowering individuals of the table, 39 *ovata*, 6 *lutea*, and 14 *brunnea*, which had not been planted out for lack of space, but confirm the results of the other set. Almost all of the plants of 1915 flowered in August. All these cultures have been conducted after the same principles, and this makes the description of further details quite superfluous.

The current view concerning the mutations of *Oenothera* is that they take place during synapsis and that the sexual cells are in the

mutated condition before the moment of self-fertilization. If we apply this to the mutability of *O. grandiflora*, we may assume that its sexual cells are divided into two main groups, about one-half remaining typical, whereas the other half belong to the type *ochracea*. Therefore the question arises, which of the triple hybrids just described are produced by the typical gametes and which by the mutated ones? In order to answer this question I made some crosses in which I used *O. grandiflora* mut. *ochracea* instead of the species itself. The *ochracea* constitutes a constant and uniform race and must obviously give the same hybrids as the mutated sexual cells of the parent species.

O. grandiflora ochracea×*O. Lamarckiana*.—I made this cross in 1914 and had two sets of seedlings in 1915, one on the bed and the other in the box. The first embraced 28 *ovata* and 2 *lutea*, the second 23 *ovata* with 3 *lutea;* together 56 plants. Those on the bed were left to flower in August and the counting was then repeated. The culture was one of the most beautiful in my garden and no doubt was possible concerning the identity of the types. Notwithstanding this, no *brunnea* and no *contraria* were observed.

O. Lamarckiana×*O. grandiflora ochracea*.—The result was exactly the same as in the reciprocal cross, but the amount of *lutea* was larger (16 specimens among 69). By the end of August almost all the plants had flowered and were carefully compared with the adjoining cultures of the first and second generations of the other crosses. It was quite evident that no *brunnea* and no *contraria* were present. Especially the *brunnea* constitute a type so widely different from the others that no error could be possible.

O. grandiflora ochracea×*O. Lamarckiana nanella*.—Cross of 1914; first generation in 1915, embracing, as in other instances, two sets, one in a box kept until the end of July and the other on the bed; observed during the whole period of flowering. There were 25 and 27 *ovata* and 5 and 3 *lutea*, but no *brunnea* nor *contraria*.

A résumé of these facts, confining the observations to those made in August at the time of flowering, is shown in table VI.

The conclusion is evident that the gametes of *O. grandiflora ochracea* produce, in their crosses with *O. Lamarckiana*, only two types, *ovata* and *lutea*. These are exactly the same, in all respects,

as the corresponding hybrids between the parent species. No *brunnea* and no *contraria* were observed. The size of the cultures fully warrants these conclusions, but is not large enough to give reliable percentage figures. From these facts it is evident that among the triple hybrids of *O. grandiflora*×*O. Lamarckiana* one type, *brunnea*, is produced only by the non-mutated gametes of the first named parent, whereas another type, *lutea*, is produced exactly by the mutated ones. If we assume that one-half of the

TABLE VI

CROSSES OF *O. grandiflora ochracea*

Cross	Culture	ovata	lutea	brunnea	contraria	Total
O. grandiflora ochracea × Lamarckiana	1915	28	2	0	0	30
O. Lamarckiana × grandiflora ochracea	1916	53	16	0	0	69
O. grandiflora ochracea × Lamarckiana nanella	1915	25	5	0	0	30
Total		106	23	0	0	129

gametes of *grandiflora* are unchanged and the other half changed into *ochracea*, one-half of the hybrids must result from the first group and the other half from the second. This shows that the pure and the *ochracea* gametes must produce each for one-half *ovata* and for the other their special hybrid. The figures, calculated in table VI, indicate 52 per cent *ovata*, 23 per cent *lutea*, and 21 per cent *brunnea*, and this corresponds as exactly as might be expected to our explanation. Thus we find:

O. grandiflora×Lamarckiana = { 50 per cent pure×Lamarckiana = 25 per cent ovata + 25 per cent brunnea; 50 per cent ochracea×Lamarckiana = 25 per cent ovata + 25 per cent lutea }

This formula may be considered to explain the empirical results of our table, since it gives 50 per cent *ovata* and 25 per cent of each of the other hybrids. The empirical figures were 52, 23, and 21 per cent, as just mentioned.

We may go still one step farther and introduce into our consideration the property of *Lamarckiana* to produce the twin hybrids,

laeta and *velutina*. These are found, on the average, in about equal numbers. Our formula now becomes:

O. grandiflora × Lamarckiana = { 50 per cent pure { × laeta = 25 per cent ovata; × velutina = 25 per cent brunnea } 50 per cent ochracea { × laeta = 25 per cent ovata; × velutina = 25 per cent lutea }

It is easily seen that this formula opens a deeper insight into the whole phenomenon of twin and triple hybrids. This point will be discussed further at the end of this paper.

O. Lamarckiana lata × *O. grandiflora*.—I made this cross twice in 1914 and 1915 and cultivated the first generation in 1915 and 1916, respectively. In the boxes it was clear that besides the hybrids described for the parent species, specimens with the type of *O. lata* were present. They had the broad leaves with rounded tops which are so characteristic of this mutant. They were planted separately and developed their typical marks during the summer. Their stems remained low and flexible, the foliage was dense, the petioles short, the blades full of bubbles and paler green than in the mutant from *Lamarckiana*. The flowers and fruits were almost like those of this mutant, but there was plenty of pollen, and the artificial self-fertilization gave a good supply of seeds. I counted (in 1915) 18 *lata* among 30 plants, and in the next year 24 among 76; together 42 among 106, or about 40 per cent, a figure which does not differ essentially from the hereditary percentages of *O. Lamarckiana* mut. *lata*. The remaining plants were mostly (41) *ovata*, with some *lutea* and some *brunnea*, some dwarfs, and some other mutants of different types. Thus we see that this cross gave exactly the results that might be expected.

In 1916 I sowed the seeds of three self-fertilized specimens of the *lata* type. The cultures showed the same splitting and the same types as in the first generation after the cross. I counted the *lata* in May and found 13, 15, and 19 per cent, and the *ovata* in May and August; they amounted to 35–51 per cent among 234 individuals. The remainder were partly *lutea* and *brunnea* and partly mutants of different types. Self-fertilized specimens of *lata* from crosses with *O. Hookeri*, *O. Cockerelli*, and *O. biennis Chicago* have given analo-

gous splittings, and the experiments just described simply confirm the conclusions drawn from them (**5,** pp. 252, 254, 255).

E. SECOND GENERATION OF CROSSES WITH O. LAMARCKIANA

As is well known, the twin hybrids from crosses of *O. Lamarckiana* are constant in their progeny, with the exception of the *laeta* from the crosses with *O. Hookeri*, which splits into *laeta* and *velutina* in the succeeding generations. For this reason I wanted to know whether the triple hybrids just described would be constant after self-fertilization or split. I found *that none of them split off one of the two others*, and in so far they were constant. On the other hand, some secondary marks, which were not observed in the first generation, turned up in the second, and thus the constancy was not absolute. Since these splittings had no significance for the main object of my study, I have not followed them up.

TABLE VII

CULTURES OF SECOND GENERATION

Cross	Cross	Second generation	ovata	lutea	brunnea	contraria
O. grandiflora × Lamarckiana	1914	1916	+	+	+	+
O. grandiflora lorea × Lamarckiana	1914	1916	+	+	+	+
O. Lamarckiana × grandiflora	1913	1916	+	−	+	−
O. Lamarckiana × grandiflora lorea	1914	1916	+	+	+	−
O. grandiflora × nanella	1913	1915	+	+	+	−
O. grandiflora × nanella	1913	1916	+	+	+	+
O. grandiflora lorea × nanella	1914	1916	+	+	+	−
O. nanella × grandiflora	1913	1915	+	−	−	−
O. lata × grandiflora	1914	1916	+	−	−	−
O. grandiflora ochracea × Lamarckiana	1914	1916	+	+	−	−
O. grandiflora ochracea × nanella	1914	1916	+	+	−	−

In respect to the third generation, it was to be expected that it would simply confirm the results of the second, and so I have limited myself to one culture for each of the three main types and to some few for the secondary combinations. Table VII gives a list of my cultures of the second generation. They embraced with some few

exceptions 60–70 specimens each, and almost all of these have flowered. As the types of the triple hybrids were exactly the same as in the first generation, no special descriptions will be necessary. In this table + means that a second generation of the type mentioned in the heading above it has been cultivated, whereas – indicates that no culture of the type has been tried.

A third generation of *ovata* was cultivated for *O. nanella*×*grandiflora*. From the reciprocal cross *lutea* and *brunnea* were continued during one generation more. I shall treat the crosses of *O. grandiflora lorea* separately, since they split off this mutant type, and deal first with the others. Among the special combinations appearing in the second generation there were three which could clearly and easily be distinguished, but only two of them were frequent. I shall designate them by the letters *R*, *T*, and *L*. Among these, *R* was a return to the rapid production of a stem, without preparatory rosette of radical leaves, which is so characteristic a mark of *O. grandiflora*, but which was always dormant in the first generation. The plants were usually slender and small, the leaves broad and dark green, and they flowered one or two weeks before their stouter sisters. In July they reached 10–30 cm. more in height than these, but during the flowering period they were overgrown by them. Their flowers showed the same forms. The progeny of the type *R* was uniformly so. The type *T* was easily recognized by its truncate flower buds; these are conical in the parental species and in the triple hybrids. The flowers were correspondingly smaller. The leaves were almost like those of *ovata*, but strikingly broader in their upper half. The height and stature were also the same. In their progeny they repeated their characters exactly, but split off some specimens of the type *R*. Type *T* was remarkably rich in the production of pitchers. The type *L* combined the characters of the hybrid called *lutea* with the slender stature, rich branching, and thin flower buds of *O. grandiflora*. It produced some specimens of *R* among its progeny, which was otherwise uniform. A continued study of these and other hybrid types of *O. grandiflora* would probably offer the material for an analysis of the characters of this species. In counting my cultures of the offspring of self-fertilized *ovata* at the beginning of the flowering period, I found the figures as given in table VIII.

The percentage figure for type *R* conforms to the formula of Mendel for monohybrids, assuming the initial rosettes to be dominant over their absence, but in the cross of *O. grandiflora* with *O. biennis* the reverse was the case. Possibly the linkage was

TABLE VIII

SECOND GENERATION OF *ovata*

Cross	Second generation	ovata	*R*	*T*	*L*	Total
O. grandiflora × Lamarckiana	1916	46	14	9	0	69
O. Lamarckiana × grandiflora	1916	60	19	2	0	81
O. grandiflora × nanella	1915	59	13	4	1	77
O. grandiflora × nanella	1916	50	16	0	0	66
O. nanella × grandiflora	1915	44	6	0	1	51
O. lata × grandiflora	1916	45	16	2	0	63
O. grandiflora ochracea × Lamarckiana	1916	39	27	6	0	72
O. grandiflora ochracea × nanella	1916	53	23	1	0	77
Total	.....	396	134	24	2	556
Percentage	.....	71	24	4.5	0.5	.....

TABLE IX

THIRD GENERATION FROM *ovata*

Cross	Second generation	Third generation				Total
		ovata	*R*	*T*	*L*	
O. nanella × grandiflora	ovata	37	25	0	0	62
" "	R	0	29	0	0	29
O. grandiflora × nanella	R	0	20	0	0	20
" "	R	0	79	0	0	79
" "	T	0	31	36	0	67
" "	T	0	3	45	0	48
" "	L	0	6	0	52	58
" "	L	0	8	0	62	70
Total	.....	37	201	81	114	433

different in the two instances. In these second generations I self-fertilized some individuals and cultivated their offspring in 1916. Table IX gives their offspring. This gives a percentage of 42 for the splitting off of type *R* from the others, and this figure seems to be analogous to the one deduced from our previous table (24 per cent). Apart from this splitting, the types *T* and *L* had a uniform progeny. The third generation of *ovata* repeated the constitution of the second in its most essential points.

The offspring of self-fertilized *lutea* consisted of this form and type *R*, but none of the other secondary types appeared among them. Table X is made up in the same way as that for *ovata*. In one instance a third generation, derived from two successive generations of *lutea*, was also studied.

TABLE X

SECOND AND THIRD GENERATION OF *lutea* CULTIVATED IN 1916

Cross	Generation	lutea	*R*	Total
O. grandiflora × Lamarckiana	2	44	25	69
O. grandiflora × nanella	2	33	12	45
O. grandiflora ochracea × Lamarckiana	2	45	11	56
O. grandiflora ochracea × nanella	2	33	15	48
O. grandiflora × nanella	3	28	51	79
Total		183	114	297
Percentage		62	38	

The percentage for *R* is 38 per cent, coinciding sufficiently with those in the two previous cases (24 per cent and 42 per cent).

As shown in table VII, I have self-fertilized specimens of *brunnea* in 7 different cultures of the first generation. I cultivated 60–70 offspring from each of them and studied them all during their whole lifetime until the first fruits began to ripen in August. One of them flowered in 1915, and one plant was fertilized so as to have a second generation of *brunnea* in 1916. It embraced 70 flowering plants. All these cultures were uniform; they produced no *R* and no others, and not even a *lorea* in the beds derived from crosses of this mutant. The same table shows three self-fertilized specimens of *contraria*, the offspring of which was studied, in 60, 70, and 72 flowering individuals in 1916. In one case there were three doubtful specimens like type *R*, but apart from these the cultures were uniform and like their parents.

We now come to the crosses of the mutant *lorea*. The special mark, consisting in the almost linear leaves, was latent in the first generation, but was seen to return in the second, whenever specimens of *ovata* or *lutea* are self-fertilized. The *brunnea*, however, did not split them off, as we have just seen. I made the following cultures (table XI) and counted them in the same way as previously

described, in the beginning of the flowering period. The percentage figures for the appearance of types *R* and *T* correspond to those derived from our table for *ovata*, which were 24 and 4.5. The figure for *lorea* is a low one, but in the cross *O. grandiflora*×*biennis* we have seen that 43 per cent *lorea* were split off in the second

TABLE XI

SECOND GENERATION OF CROSSES OF *O. grandiflora lorea;* CULTURES OF 1916

Cross	Second generation	ovata	lutea	*R*	*T*	nanella	lorea	Total
O. grandiflora lorea×Lamarckiana	ovata	54	.....	25	7	0	6	92
O. grandiflora lorea×Lamarckiana	lutea	.....	51	4	0	0	28	83
O. Lamarckiana×grandiflora lorea	ovata	58	.....	26	10	0	2	96
O. Lamarckiana×grandiflora lorea	lutea	.....	68	2	0	2	9	81
O. grandiflora lorea×nanella	ovata	51	.....	15	3	0	2	71
O. grandiflora lorea×nanella	lutea	.....	50	6	0	1	9	66
Total	.....	163	169	78	20	3	56	489
Percentage	.....	68		16	4	1	11	.....

generation. The question whether this phenomenon conforms to the formula of Mendel for monohybrids remains to be answered by more extensive cultures.

F. MASS MUTATIONS, CONSIDERED AS SECONDARY MUTATIONS

After describing the facts observed in my cultures and experiments, we may now proceed to the discussion of the principle of BARTLETT, already quoted. He assumed that a fundamental mutation occurred in one of the two gametes in a generation preceding that in which the mass mutation appeared. We are not concerned, however, with the question whether all instances of mass mutation are due to the same internal processes, but only with the problem of explaining the production of mut. *ochracea* from *O. grandiflora* by means of BARTLETT'S suggestion.

In order to proceed in an empirical way, and to rely as much as possible on analogy with well ascertained facts, I shall start from

a consideration of the mutation of *O. Lamarckiana gigas* into its dwarf mutants (**8**). These spring from the self-fertilized strain of *O. gigas* in about 1–2 per cent of the offspring of every generation, and have done so since the very origin of the parent form. Artificially crossed with their parent, they produce hybrids of high stature, which are not externally distinguishable from *O. gigas* itself, and which split, in the next generation, into three types, according to the formula of Mendel for the monohybrids. Assuming, as is now generally conceded, that mutations take place before fecundation, we can easily see that the gametes of *O. gigas* which mutated into *nanella* must for some part be united in fecundation with normal sexual cells. Such combinations must produce half mutants, as I called them in my book *Gruppenweise Artbildung*,[6] or mutant hybrids, as they have since been called (**8,** p. 345), and these will split in the next generation into about one-fourth dwarfs, one-fourth high and normal *gigas*, and one-half new mutant hybrids. The latter will continue to reproduce the splitting in the succeeding generations, and this may obviously be repeated during an unlimited number of successive years.

If we now suppose that, by means of some contrivance, the dwarfs and the constant high specimens were yearly eliminated before flowering, we should have a race which would produce in every generation about one-fourth dwarfs. The phenomenon would then be an instance of mass mutation, and we may choose it as the prototype from which to explain our observations on *O. grandiflora*. From our point of view the splitting would be a repeated appearance of the dwarf mutants, due to the original mutation of one gamete. For this reason we shall call it a *secondary mutation*.

Let us now consider the strain of *O. grandiflora*, found in 1912 near Castleberry, Alabama, as such a mutant hybrid, originally produced by the mutation of a sexual cell into *ochracea* and its copulation with a normal gamete of the strain. Whether this initial mutation took place a few or many years before 1912 is of course without interest for this discussion. It may even be older

[6] The case is especially clear in the instance of *O. Lamarckiana semigigas*, where the half mutants with their 21 chromosomes are obviously the result of the copulation of normal gametes with others mutated into *gigas*.

than the species itself. We further assume a close analogy with the mutant hybrids of *O. gigas nanella*. This conduces to the expectation of three types in every generation, namely, constant *ochracea*, constant *grandiflora*, and hybrid mutants.

The *ochracea* are our secondary mutants; they were seen to arise in my cultures constantly during the three generations of my experiments, and every time in large numbers. The mutant hybrids are the apparently normal specimens of *grandiflora* of my strain; they repeat the splitting in every generation, but no constant *grandiflora* have been found, since all the specimens tried reproduced the mass mutation. Here, therefore, we have to introduce another principle. This is the assumption of a lethal factor. MORGAN and his students have discovered the presence of four such units in their experiments with *Drosophila*, and from their studies we know exactly what to expect from them (11). I have already proposed this principle for the explanation of the empty seeds of *O. Lamarckiana* (4), and we may apply it here in the same way. I determined the amount of barren grains among the seeds of my strain of *O. grandiflora* and found 12–41 per cent, with an average of 25 per cent for the harvest of 8 self-fertilized plants of different generations (4, table on p. 245). Now our argument led us to expect 25 per cent of constant specimens, and the hypothesis that these are killed within the seeds by some lethal factor would at once explain their absence and the presence of the barren grains.

By means of this hypothesis the conception of our strain of *O. grandiflora* as a hybrid mutant now becomes complete. It starts from two succeeding initial mutations in sexual cells, which copulated with normal ones. One of these was the mutation into a weak, yellowish *ochracea*, the other was the production of a lethal factor, linked to the non-mutated gametes. This linkage must be assumed to be so complete as not to interfere with the applicability of Mendel's formula for monohybrids.

The presence of the lethal factor in both the gametes of a copulation kills the germ after some time, but the presence of the same factor in only one of the two gametes leaves them viable. This latter proposition is proved by numerous crosses between species with barren grains and those without the factor in question. Such seeds are always capable of normal development.

The supposed initial mutations of our strain, therefore, must have produced half mutants, the gametes of which split in every generation into about equal parts of potential *grandiflora* with the lethal factor, and into viable *ochracea*. The fecundation must then produce one-fourth of germs of *grandiflora* with the double lethal factor and thereby doomed to die off within the seed; one-fourth of viable but weak *ochracea*, which will be constant in their progeny; and one-half of hybrids between the two mutants, in which the qualities of the type of the species will be dominant, whereas the lethal factor must be recessive.

Among the living seedlings the proportion of green hybrid mutants and yellowish *ochracea* must therefore be 2:1, and the average figure for the latter was 26 per cent, although this was somewhat too low on account of the loss of part of the yellow seedlings in early youth. Artificial crosses between the hybrid mutants and the *ochracea* should give about 50 per cent of either type. I found for both the reciprocal crosses about 34 per cent, but the figure was depressed from the same cause. A repetition of these experiments, excluding the influence of these losses, is proposed; it is expected to give a fuller proof.

We assume the supposed initial mutations to have been analogous to the mutations into *lorea* and *gigas*, which may still be observed to occur in my garden. New mutations into *ochracea* may occur also, but they must evidently always escape observation, being different in no respect from the secondary or mass mutation.

BARTLETT has pointed out the analogy between the phenomenon of mass mutation and Mendelian splitting, observing, however (1, p. 452), that "there can be no doubt that mass mutation is not Mendelian segregation, although the two phenomena have points of resemblance." In our instance this resemblance is plain enough, but a splitting is called Mendelian if it is observed among the progeny of hybrids between different species, varieties, or strains, whereas the half mutants are hybrids between mutated and non-mutated sexual cells of the same parent. They are produced by one experimental pure line, whereas real hybrids are the result of the combination of different strains. The hybrid mutants start from a mutation; they can never be made use of as an argument against

the mutation theory. The names of mass mutation and secondary mutation, therefore, seem to be very appropriate, indicating, as they do, the true explanation of the phenomenon.

G. TWIN HYBRIDS, CONSIDERED AS A RESULT OF MASS MUTATION

In *Gruppenweise Artbildung* (5) I have devoted a large part to the study of the twin hybrids of *O. Lamarckiana* and its derivatives in their crosses with other species. I was convinced that some relation must exist between the cause of this curious phenomenon and the high degree of mutability of the species. I supposed this internal cause, whatever it might be, to be responsible in a large degree, not for the mutability itself, since this is not a special trait of the *Lamarckiana*, but for the exceptionally high degree of development of the quality in that species.

Later investigations of different authors, and especially those of RENNER, have confirmed this conception, since they do not offer an explanation of the problem involved on the basis of other exceptional qualities of my plant. The experiments described for *O. grandiflora*, however, prove that there is still another relation, since the twins may be considered as the result of the fecundation of sexual cells which are, for a large part, in the condition of mutated gametes. It is evident that in crosses these latter may give different hybrids from those of the normal gametes of the same parent. I shall now try to show that the results of my crosses confirm this view in almost all their details.

We have to start from the assumption that the mass mutations take place in the same numerical proportions as those required by the formula of Mendel for monohybrids; in other words, that the two kinds of gametes are produced in equal numbers and among the pollen as well as among the egg cells. Fecundation with a different species must then produce two kinds of hybrids, each of them in about 50 per cent of the offspring. Our table for the production of *laeta* and *velutina* in such crosses gave on the average 52 per cent for the first and 46 per cent for the latter, and thus fully confirms our conception. When the crosses are repeated with mut. *ochracea* instead of the type of the species itself, no twins must be the result, but only uniform hybrids of the type corresponding with

the *laeta*. Until now I have tried only one instance, *O. grandiflora* × *O. Cockerelli* and its reciprocal. They produced only one of the twins, namely, *laeta*, and thus confirm our view. Other combinations should be studied for the same purpose.

If Mendel's law were applicable to the production of the twins, these must split after self-fertilization into three or more types. Our table shows that this is not, or at least not always, the case. The *velutina* never split, nor do the *laeta* of *O. biennis*, *O. syrticola*, and *O. biennis Chicago* produce a splitting. Only those of *O. Cockerelli* show this phenomenon, but here it is limited to the repetition of the mass mutation into *velutina*. From these facts we must conclude that the hereditary factors involved are not in the condition required by Mendel's laws. In *Gruppenweise Artbildung* I have called this deviating condition labile, leaving the question open whether it may be determined by means of linkage or otherwise.

The cross of the pollen of *O. grandiflora* with the female gamete of *O. biennis Chicago* produces twins which are quite different from the *laeta* and *velutina*, and are therefore called *densa* and *laxa*. Formerly I assumed this difference to be due to the splitting of another factor, but my results with *O. grandiflora*, in connection with the appreciation of the complicated nature of so many mutations (7), open the prospect of considering it as due to the same unit, only under the influence of different linkage. In fact, if we assume the pollen of *O. grandiflora* to be dimorphous before fecundation, two types of hybrids must be expected in this cross as well as in others. This conception simplifies the problem, although it does not offer a direct proof against the presence of a special splitting factor for *densa* and *laxa*. These twins are constant in their progeny, even as the *laeta* and *velutina* just considered, and thereby indicate the same special condition of the factors involved. Whenever the differentiating characters of the twins are recessive to those of the other parent, the twins must show the same external marks. The hybrids will then be uniform instead of dimorphic, as, for example, in our experiment with *O. grandiflora* × *O. syrticola* (*muricata*).

The cross *O. grandiflora* × *O. biennis* gave a dimorphic progeny, which may evidently be ascribed to the presence of mutated and

normal gametes in the first species. If we assume this to be the true interpretation, the pedigree may be written in this form:

O. grandiflora×*biennis*, or

O. grandiflora typica×*biennis*+*O. grandiflora ochracea*×*biennis*

First generation— *biennis* *ochracea*

Second generation— *biennis* *ochracea* *ochracea biennis*

Read in this way our experiments show that in the normal gametes of *O. grandiflora* the characters of the species are recessive to those of *O. biennis*, and that uniform and constant hybrids are produced. The gametes which repeated the mutation into *ochracea*, on the other hand, possessed dominant characters, and the offspring was hardly distinguishable from normal *ochracea*. But after self-fertilization it split off the *biennis* type, especially the character of producing stout initial rosettes before making a stem, and this splitting seems to conform to Mendel's law for monohybrids.

H. ANALOGY BETWEEN THE TWINS OF O. GRANDIFLORA AND O. LAMARCKIANA

In concluding this article I might point out the striking analogy between the splitting phenomena of *O. grandiflora* and those of *O. Lamarckiana*. Evidently they must be considered as the results of the same internal causes. The chief difference is the absence of a visible mass mutation in the latter species. On the contrary, the amount of barren grains among its seeds is double that of *O. grandiflora*. We are therefore induced to assume a second lethal factor, linked with the characters of *ochracea* and *laeta*, respectively, and killing the *laeta* germs of *O. Lamarckiana*. Or, stating it in other words, we may imagine the factor for weakness, which causes the death of a large part of the *ochracea* mutants after germination, to be replaced in *O. Lamarckiana* by a lethal factor, which kills the corresponding germs before germination.

RENNER (12) has proposed an explanation which in some respects parallels the views developed in this article, but, as I have

already explained, it differs mainly in the conception of the first origin of *O. Lamarckiana*. RENNER considers this species to be a hybrid between two previously existing types, corresponding to *laeta* and *velutina*, and sees in this hybrid condition the cause of its mutability. The analogy with *O. grandiflora* leads us, however, to consider this "hybrid condition" not as the cause but as a result of the mutability. Elsewhere I have shown that his conception leads to contradictions and requires too many additional hypotheses, even without considering the analogy with *O. grandiflora* (4). A detailed criticism of RENNER'S views from this latter standpoint, however, must be postponed until another opportunity.

Summary

1. *Oenothera grandiflora* Aiton from Castleberry, Alabama, splits in my cultures in every generation into two types. One of them consists of strong, green plants of the parent type; the other of weak, yellow individuals, of which only a few are vigorous enough to flower and ripen their seeds. This weak type is called *O. grandiflora* mut. *ochracea*.

2. Besides these it produces other mutants in the ordinary proportions of 0.1–1 per cent, namely, mut. *lorea* with almost linear leaves and mut. *gigas* with 28 chromosomes and the corresponding stoutness of all its organs. These two types are constant from seed, but the *gigas* keeps on mutating into *lorea* and *ochracea*.

3. The crosses among *O. grandiflora*, *O. ochracea*, and *O. lorea* show that these forms are isogamic, the pollen carrying the same hereditary qualities as the egg cells.

4. *O. grandiflora* yields twin hybrids with the same species which produce twins in their combinations with *O. Lamarckiana*. The female organs of *O. biennis*, *O. syrticola* (*muricata*), *O. suaveolens*, the pollen of *O. biennis Chicago*, and both sexes of *O. Cockerelli* split *O. grandiflora* into *laeta* and *velutina*, whereas the cross *O. biennis Chicago*×*grandiflora* yields the twins *densa* and *laxa*. The twins appear, on the average, in about equal numbers. This splitting fails when the crosses are made with mut. *ochracea* instead of *O. grandiflora*. Their progeny is uniform and corresponds, so far as investigated, to the *laeta* among the twins.

5. In other crosses of *O. grandiflora* the hybrids also resemble the corresponding ones of *O. Lamarckiana*. *O. grandiflora*×*syrticola* produces the type *gracilis*, *O. grandiflora*×*biennis* hybrids of the types of *biennis* and *ochracea*, among which the first is constant in its progeny, whereas the second repeats the splitting.

6. In crosses with *O. Lamarckiana*, *O. grandiflora* produces combinations of the two groups of twins. I found three such types. One of them embraces about one-half of the offspring and corresponds to the *laeta;* it is called *ovata*. The two others appear each in one-fourth of the whole culture and are called *lutea* and *brunnea*. The first corresponds to the combination *ochracea*×*velutina*, the second to *grandiflora*×*velutina*. These triple hybrids are constant in their progeny, inasmuch as they do not produce individuals of the other types, but split off some forms which constitute different combinations of the parental characters and partly also of those of the mutants. One of them, lacking the initial rosette of radical leaves, appears in percentage figures which seem to correspond to the formula of Mendel for monohybrids.

7. If the crosses are made with the mutant *lorea*, this character is latent in the first generation and reappears in the second in about one-quarter of the individuals; but this rule shows some exceptions.

8. From these facts, in combination with the occurrence of about 25 per cent of barren grains among the seeds, we arrived at the conclusion that the yearly production of large numbers of *ochracea* is a phenomenon of mass mutation, analogous to the instances described by BARTLETT and due to an initial mutation of the ordinary rare type, followed by secondary mutation in the succeeding generations.

9. This initial mutability of *O. grandiflora* must have yielded, besides the ordinary mutants, hybrid mutants, produced by the combination of a mutated sexual cell with a normal one. If then the offspring of this fecundation is assumed to split in a manner analogous to Mendel's formula for monohybrids, three types must be the result. One of them is the mut. *ochracea*, which is now a secondary mutant; the second is the mutant hybrid of the type of the species, which will repeat the splitting; and the third must be a constant form of the same type. This last does not appear, and

a lethal factor is assumed to answer for this gap. It must be linked to the otherwise pure *grandiflora* gametes. It explains the absence of the constant type, together with the presence of a corresponding percentage of empty seeds.

10. In this way the mass mutation as well as the empty grains can be explained by the assumption of two initial mutations of the ordinary type. One is that into *ochracea*, the other is the origin of a lethal factor linked to the gametes which are not mutated into a weak, yellow form.

11. The twin hybrids, mentioned under 4, must be the result of the same secondary splitting of the gametes. Those of the *grandiflora* type must yield the *velutina* and the *laxa;* those carrying the characters of *ochracea* must give the *laeta* and the *densa*.

12. The twins produced by the crosses of *O. grandiflora* with *O. biennis*, *O. syrticola*, and *O. biennis Chicago* are constant in their progeny, but the *laeta* from crosses with *O. Cockerelli* repeat the splitting into the types of the twins.

LUNTEREN, HOLLAND

LITERATURE CITED

1. BARTLETT, H. H., Mass mutation in *Oenothera pratincola*. BOT. GAZ. **60**: 425–456. 1915.
2. ———, Mutations en masse. Amer. Nat. **49**:129. 1915.
3. DAVIS, B. M., Genetical studies on *Oenothera*. Amer. Nat. **44**:108–115. 1901; **45**:193–233. 1911.
4. DEVRIES, H., Gute, harte, und leere Samen von *Oenothera*. Zeitschr. Indukt. Abst. Ind. Vererbungs. **16**:239. 1916.
5. ———, Gruppenweise Artbildung. Berlin. 1913.
6. ———, On triple hybrids. BOT. GAZ. **47**:1–8. 1901.
7. ———, Die endemischen Pflanzen von Ceylon und die mutierenden Oenotheren. Biol. Centralbl. **36**:1–11. 1916.
8. ———, *Oenothera gigas nanella*, a Mendelian mutant. BOT. GAZ. **60**:337–345. 1915.
9. ———, On twin hybrids. BOT. GAZ. **44**:401–407. 1907.
10. GATES, R. R., Recent papers on *Oenothera* mutations. New Phytol. **12**: 296–302. 1913.
11. MORGAN, STURTEVANT, MULLER, and BRIDGES, The mechanism of Mendelian heredity. New York. 1915.
12. RENNER, O., Befrüchtung und Embryobildung bei *Oenothera Lamarckiana*. Flora **7**:115–150. 1914.

NOTES ON NORTH AMERICAN TREES. I. QUERCUS

C. S. SARGENT

QUERCUS TEXANA Buckley.—The type of this species grows on dry limestone hills in the neighborhood of Austin, Texas. Here it is a small tree not more than 7–10 m. high and often a large shrub rather than a tree. The branchlets are slender, glabrous or rarely pubescent, and red or reddish in color, and the winter buds are ovate, acute, with reddish, slightly or densely pubescent scales, and usually 4–6.5 cm. in length. The leaves, which are usually of the same shape on upper and lower branches, are deeply divided by broad sinuses rounded in the bottom into 5–7 lobes, the upper lobe 3-lobed at apex, the lateral lobes broad and more or less divided at apex into acuminate lobes, with the exception of those of the lowest pair which are much reduced and less deeply lobed; the base of the leaf is broadly cuneate or concave-cuneate. The leaves are only occasionally furnished on the lower surface with small axillary tufts of pale hairs; when they unfold they are thickly coated on both surfaces with pubescence and are often bright red. On the small trees growing on the dry hills of central Texas the acorn is about 1.5 cm. long and inclosed for one-quarter to one-half its length in a turbinate cup covered with thin, closely appressed, pubescent scales rounded at the narrow apex. Descending sometimes from the hills into better soil, the Texas oak grows taller and produces fruit occasionally 2.5 cm. in length, with a turbinate cup comparably less deep than that of the smaller fruit produced on the neighboring hills. On the Edwards Plateau in western Texas trees occur with acorns acute at apex, about 2 cm. long and only 7 or 8 mm. in diameter. On some trees in this region the leaves are 5-lobed with broad shallow sinuses. The following forms from western Texas can be distinguished:

✓ QUERCUS TEXANA var. **chesosensis,** n. var.—Differing from the type in the acuminate lobes of the leaves and smaller cups.

Dry rocky lower slopes of the Chesos Mountains, Brewster County, Texas, *G. B. Sudworth*, November 15, 1913.

The leaves of this variety are oblong to oblong-obovate in outline, broadly cuneate or occasionally sharply cuneate at base, divided by broad sinuses rounded in the bottom into 5 or 7 narrow acuminate spine-tipped lobes, the lateral entire, the elongated terminal lobe slightly 3-lobed at apex; they are thick, lustrous on the upper surface and glabrous or sometimes pubescent below, furnished with small axillary tufts of hairs, 5–10 cm. long and 2–8 cm. wide, the terminal lobe of the larger leaves being sometimes 5 cm. in length; petioles slender, glabrous, often tinged with red, 5–15 cm. long. The nut is about 8 mm. long and 5 mm. in diameter, pointed and tomentose at apex, and inclosed for one-quarter of its length in a turbinate cup covered with the thin scales rounded at apex of *Q. texana*.

It is a shrub or small tree with slender, glabrous, bright orange red branchlets becoming reddish brown in the second year, and acute winter buds 4–5 mm. long covered with brown more or less tomentose scales. It is possible that this is the oak from the mouth of the Pecos River described by TORREY (Bot. Mex. Bound. Surv. 206. 1858) as *Q. coccinea* var. *microcarpa*.

A specimen of a plant which differs only from those from the Chicos Mountains in the darker color of the branchlets was collected by *Buckley* in 1875 near Fort Davis, in Jeff Davis County, Texas. The shape of the leaves of these trees is very different from those of *Q. texana* of central Texas, and in spite of the similarity of the fruit it may be possible, when more material is available, to separate this form specifically.

QUERCUS TEXANA var. **stellapila,** n. var.—Differing from the type in the clusters of fascicled hairs which cover both surfaces of the mature leaves and the branchlets of the year.

Sproul's Ranch above Fort Davis, Davis County, Texas, alt. 2000 m., *D. M. Andrews* (no. 74, type), August 25, 1913.

The leaves of this variety, which is a small tree, are thick, dark bluish green above, yellowish below, oblong-obovate, acuminate at apex, cuneate or occasionally rounded at base, and divided by wide shallow sinuses rounded in the bottom into broad usually entire acute lobes. They are 7–12 cm. long and 5–7 cm. wide; petioles slender, 5–6 cm. in length. The fruit, although slightly larger, cannot be distinguished from that of var. *chesosensis*. This tree in the shape of the leaves, their short petioles, and in the persistent fascicled hairs which cover them and the branchlets is the most distinct of the forms which I refer to *Q. texana*.

In the paper in which he described *Quercus texana* BUCKLEY described another Texas oak:

QUERCUS SHUMARDII Buckley, Proc. Acad. Nat. Sci. Phil. 1860. 444.—*Quercus rubra* var. *texana* Buckley, *loc. cit.* 1881. 123.—This is a large tree of low woods, with grayish or grayish brown

branchlets and oblong-ovate acute winter buds 5–6 cm. in length, covered with glabrous or rarely slightly pubescent yellowish brown scales scarious on the margins. The leaves are always furnished below with large conspicuous tufts of hairs in the axils of the veins and on the upper branchlets are deeply divided by broad sinuses into narrow acute lobes, and although often larger resemble in shape those of *Q. texana*, but the lower leaves are 7-lobed with short broad lobes separated by narrow sinuses pointed or rounded in the bottom, and are often 15–20 cm. long and 10–12 cm. wide, and are broadly acuminate or truncate at base. The nuts are oblong-ovate, narrowed and rounded at apex, frequently 3 cm. long and 2 cm. in diameter, the base only inclosed in a shallow saucer-shaped cup covered with thin or often with conspicuously tuberculate pale pubescent or nearly glabrous scales. Leaves of sterile branchlets from the tops of this tree are often difficult to distinguish from those of *Q. texana*, and the best characters by which these oaks can be distinguished are found in the red brown more or less pubescent buds and reddish branchlets of *Q. texana* and its varieties, and in the usually glabrous grayish buds and grayish branchlets of *Q. Shumardii* and its variety. The close relationship of these trees is shown, however, in the occasional occurrence in Missouri of trees of *Q. Shumardii* with reddish, slightly pubescent buds and reddish branchlets.

Quercus Shumardii ranges from eastern Texas through the valley of the Mississippi River to northern Missouri, southern Illinois and Indiana, and western Ohio, and through the Gulf and south Atlantic states to North Carolina. Under favorable conditions it becomes one of the largest of American oaks, and individuals up to 40 m. in height with trunks 1.5 m. in diameter and much buttressed at the base are not rare. Trees with the much thickened and with the thin cup-scales grow together over the whole region occupied by this species. The fruit with thin cup-scales is often difficult to distinguish from that of the northern red oak, and it is *Q. Shumardii* which has often been mistaken for it in the eastern Gulf states, where the northern tree is extremely rare, and in southern Missouri and in Texas, where it does not appear to grow.

On the trees with the saucer-shaped cups others occur with deep cup-shaped cups. This is the *Q. Schneckii* Britton, and as the trees with the shallow and with the deep cups do not otherwise differ, the latter is best considered a variety of the former. If this view is adopted it becomes

QUERCUS SHUMARDII var. **Schneckii,** n. var.

QUERCUS TEXANA Sargent, Silva N. Am. 8:129 (in part). 1895 (not Buckley).—*Q. Schneckii* Britton, Man. 333. 1901.—Differing from the type in the cup-shaped cups of the fruit covered with thin or rarely toward the base with much thickened scales.

This is the more common form in the Mississippi valley, and although not rare in the Gulf and south Atlantic states, it is less common there than the type. Forms with thickened cup-scales I have seen only on specimens collected by *T. G. Harbison* "from large wide-spreading trees in low rich soil in river bottoms north of Vicksburg, Mississippi," October 27, 1916.

QUERCUS COCCINEA Moench.—An interesting form of the scarlet oak may be distinguished as

QUERCUS COCCINEA var. **tuberculata,** n. var.—Differing from the type in the much larger fruit, with cup-scales more or less thickened below the middle of the cup-shaped or turbinate cup, those of the upper row thin and forming a distinct marginal ring.

Bluffs of the Alabama River, near Berlin, Dallas County, Alabama. *C. S. Sargent*, April 19, 1915; *R. S. Cocks*, August 27, 1915 (no. 912), September 1, 1915 (no. 940), August 24, 1916 (no. 898, type).

In the habit of this oak, which is a large tree, in the bark of the trunk, and in the leaves there is nothing to distinguish it from the typical *Q. coccinea*. The location is exceptional, for this tree ranges south along the Appalachian Mountains and their foothills, and has not been found before east of the Mississippi River south of northern Georgia and northeastern Mississippi. In other parts of the country the cup-scales of *Q. coccinea* sometimes show a tendency to thicken, although in a less degree than those on these Alabama trees; and I have seen specimens with such thickened scales from a tree growing near New Bedford, Massachusetts, and on one from Tennessee without exact locality.

QUERCUS RUBRA L.—The specimen on which LINNAEUS based his *Q. rubra* (*Q. falcata* Michx.) came from Virginia and has ovate to obovate long-stalked leaves narrowed and rounded or cuneate at base, with a long acuminate entire or slightly lobed terminal lobe and 2 or 4 large acuminate lateral lobes pointing forward. Leaves of this form, which must be considered the typical form of *Q. rubra*, are pubescent early in the season on the upper surface, becoming nearly glabrous before autumn. The lower surface is covered more or less thickly with rusty or pale pubescence. This is the common form of the southern red oak in the Atlantic states north of Virginia. On some trees leaves occur which are broadly

obovate and 3-lobed at apex, with rounded or acute lobes, the terminal lobe being sometimes slightly lobed, and are rounded or cuneate at base. On some individuals all the leaves are 3-lobed and these may be distinguished as

QUERCUS RUBRA var. TRILOBA Ashe, Proc. Soc. Am. Foresters **11**:90. 1916.—*Q. cuneata* Wangenheim, Nordam. Holz. 78. *pl. 5. fig. 14.* 1787; *Q. triloba* Michx. Hist. Chênes Amér. no. 14. *pl. 26.* 1801; *Q. rubra* Abbott and Smith, Insects of Georgia, **1**:99. *pl. 50.* 1797 (not Linnaeus); *Q. falcata β triloba* Nutt. Gen. **2**:241. 1818. —The leaves of this variety vary from 5 to 8 cm. in length and from 4 to 9 cm. in width, and are glabrous on the upper surface and grayish or yellowish pubescent on the lower surface. So far as I have observed, this variety of the southern red oak does not grow to a large size, and trees more than 10–15 m. tall are not common.

It is nowhere abundant, and the only specimens from the northern states which I have seen were collected by *J. K. Small* in the vicinity of Pleasant Grove, Lancaster County, Pennsylvania, in June 1881, and by *Charles C. Deam* in Jefferson County, Indiana (nos. 16, 253, 18775). On dry uplands near Milledgeville in central Georgia it is the common form of red oak. I have not seen specimens from Louisiana, and only one specimen collected by *E. J. Palmer* (no. 12765) near Houston, Harris County, Texas, from any part of the region west of the Mississippi River.

A form of the southern red oak with oval or oblong leaves deeply divided into 5–11 acuminate often falcate lobes and white-tomentose below may best be considered, as ELLIOTT who first noticed this tree considered it, a variety which now becomes

QUERCUS RUBRA var. PAGODAEFOLIA Ashe, Proc. Soc. Am. Foresters **11**:90. 1916.—*Q. falcata* var. *β pagodaefolia* Elliott, Sk. **2**:605. 1824; *Q. pagoda* Rafinesque, Alsograph. Am. 23. 1838; *Q. pagodaefolia* Ashe, BOT. GAZ. **24**:275. 1897; Sargent, Man. 244. *fig. 197.* 1903.

At one time I believed that this oak might be distinguished specifically from *Q. rubra*, basing my opinion on the paler bark of the trunk, on the shape of the leaves with more numerous and more acuminate lobes, often repand-dentate at the apex, on the whiter pubescence on their lower surface, and on the fact that this tree often grows in lower situations and in moister soil than those which *Q. rubra* selects; but further field observations show that these characters cannot be depended upon. Trees of the two forms grow in low ground and on

uplands. Pale bark occasionally occurs on trees of the typical form and dark bark on trees with the leaves of var. *pagodaefolia*, and leaves typical of the two forms are often found on the same tree.

An oak which has long puzzled the students of our southern trees who have tried to refer it as an extreme form to *Q. rubra* var. *pagodaefolia* has recently been distinguished by ASHE as

QUERCUS RUBRA var. LEUCOPHYLLA Ashe, Bull. Charleston Mus. 13:25. 1917.—Differing from the type in the shape of the leaves, on upper branches nearly as broad as long, deeply divided into 5–7 broad lobes and brownish pubescent below, on lower branches slightly obovate, less deeply divided and only slightly pubescent on the lower surface.

The fact that the leaves on the upper and lower parts of the tree are different, as ASHE points out, has added to the difficulties of understanding this tree. The leaves on upper branches are deeply 5–7-lobed, being broader at the apex than those of var. *pagodaefolia;* they are rounded at base, thick, glabrous on the upper surface and more or less thickly coated below with brownish pubescence, and are usually 10–15 cm. long and 9–15 cm. wide. The leaves on lower branches are slightly obovate, rounded or cuneate at base, and usually 7-lobed; the terminal lobe is acute or rounded and often slightly 3-lobed toward the apex; the lateral lobes of the upper pair are much larger than the others and often slightly lobed at the broad apex; those of the lower pairs are nearly triangular and acute. These leaves are thin, dark green, sometimes pubescent, becoming glabrous on the upper surface, sometimes thickly covered with pale or brown pubescence on the lower surface, and are often 12–25 cm. long and 10–20 cm. wide. Occasionally trees occur on which the leaves are obovate, gradually narrowed from below the middle into a long cuneate base, and only slightly lobed toward the apex with entire acuminate lobes. HARBISON has observed that the hilum of the nut of this variety is pink and that the hilum of other forms of *Q. rubra* is always yellow.

This form of red oak is a large tree, 30–40 m. high, and is found from the coast of Virginia to northern Florida, and through the Gulf states to eastern Texas, ranging northward to northern Arkansas, where it appears in a form in which the lobes of the leaves are rather narrower than those on trees farther south, thus approaching var. *pagodaefolia*. This form of the southern red oak is common in the low woods about River Junction, Florida, where it grows to a very large size, and in central Mississippi. Often the leaves on the lower branches cannot be distinguished by their shape and pubescence from those of *Q. velutina*, and specimens have been referred to that species.

QUERCUS NIGRA L.—In the shape of the leaves the water oak is one of the most variable of the oaks of the United States. In

what must be considered the type of the species, as LINNAEUS based his description on GRONOVIUS' "Quercus foliis cuneiformibus obsolete trilobis" and on CATESBY'S figure (Nat. Hist. Car. 1: *pl. 20*), the leaves are oblong-obovate, gradually narrowed and cuneate at base and enlarged often abruptly at the broad rounded entire or occasionally obscurely 3-lobed apex. On trees with such leaves, and especially on vigorous young branchlets, the leaves are sometimes pinnatifid with acute, acuminate, or rounded lobes, or are deeply 3-lobed at apex, or are broadly oblong-obovate and rounded at apex with entire or undulate margins. Occasionally on upper branches a linear-lanceolate leaf similar in shape to those of seedling plants can be found. The leaves of the seedlings differ more from the leaves of older trees than in any other of our oaks, and are linear-lanceolate with entire or undulate margins, or are occasionally lobed with one or two pointed lobes, and are often deeply 3-lobed at the broad apex with acuminate rounded lobes; such leaves are occasionally furnished below the middle with a single acuminate lobe, leaves of all these forms often occurring on one plant less than 1 m. tall. On occasional mature trees all the leaves are trilobed at the apex, and such leaves appear so different from the common form of the water oak that this form may be distinguished as

QUERCUS NIGRA var. **tridentifera,** n. var.—Differing from the type in the oblong-obovate leaves, gradually narrowed below into an elongated cuneate base and gradually widened above into a more or less deeply 3-lobed apex, the lobes rounded or acute.

LOUISIANA.—Near Laurel Hill, West Feliciana Parish, *Cocks* and *Sargent*, April 13, 1916 (type); Loranger, Tangipahoa Parish, *Cocks* and *Sargent*, March 30, 1917; Audubon Park, New Orleans, *R. S. Cocks*, October 8, 1913, *C. S. Sargent*, March 31, 1917.

MISSISSIPPI.—Liberty Road, near Natchez, Adams County, Miss *C. C. Compton*, April 19, 1915; near Jackson, Hinds County, *T. G. Harbison* (no. 82), May 20, 1915.

ALABAMA.—Roadsides near Selma, Dallas County, *C. S. Sargent*, April 19, 1915.

TEXAS.—Navidad River, Lavaca County, low woods, *E. J. Palmer* (no. 9237), March 20, 1916 (no. 9086, with some leaves acute and laterally lobed), March 6, 1916.

VIRGINIA.—Near Suffolk, Nansemond County, *A. Rehder*, August 18, 1908.

On the tree at Loranger, Louisiana, a few of the leaves are elliptical to oblong-obovate, entire and acuminate at the ends. On COCKS's specimens from New Orleans the leaves at the base of the branches are broad at the apex and distinctly 3-lobed with rounded lobes, and the lobes are narrow and long-acuminate and are often also laterally lobed.

Quercus microcarya Small appears to be only a depauperate form of var. *tridentifera*, which may be called

QUERCUS NIGRA var. TRIDENTIFERA f. **microcarya,** n. f.—*Q. microcarya* Small, Bull. Torr. Bot. Club **28**:357. 1901.—Differing from *Q. nigra* var. *tridentifera* in its smaller leaves and fruit and in its dwarf habit.

Crevices in the rocks and in thin dry soil on the slopes of Little Stone Mountain, Dekalb County, Georgia.

Quercus rhombica, n. sp.—Leaves rhombic, rarely oblong-obovate to lanceolate, acute or rounded and apiculate at apex, cuneate at base, the margins entire and slightly undulate, on vigorous shoots occasionally furnished near the middle with a pair of short broad or rounded lobes; when they unfold, deeply tinged with red, covered with short pale caducous pubescence, and furnished below with more or less conspicuous usually persistent tufts of axillary hairs, and at maturity thin, dark green and lustrous on the upper surface, pale on the lower surface, 9–12 cm. long and 3.5–5 cm. wide, with stout conspicuous yellow midribs and slender primary forked veins; turning yellow and falling gradually in early winter; petioles yellow, 5–12 mm. in length. Flowers not seen. Fruit ripening at the end of the second season, sessile or short-stalked; nut ovate, rounded at apex, thickly covered with pale pubescence, about 1 cm. long and 1.5 cm. in diameter, with a thin shell lined with hoary tomentum and pale orange colored cotyledons; cup saucer-shaped to cup-shaped, rounded on the bottom, silky pubescent on the inner surface, the scales reddish brown, rounded at apex, slightly pubescent, loosely appressed with free tips, those of the upper rank thin and ciliate on the margins.

A tree often 40–50 m. high, with a tall trunk 1–1.5 m. in diameter, covered with pale slightly furrowed bark, stout wide spreading smooth branches forming a broad head, and slender glabrous branchlets red brown in their first season and dark gray the following year.

Borders of swamps and low wet woods of the coast region from the Dismal Swamp, Virginia, to eastern Texas; common, especially in southern central Alabama and in Louisiana, where in the western part of the state it extends north of the Red River.

VIRGINIA.—Dismal Swamp, *L. F. Ward*, 1887 (distributed as *Q. aquatica* var. *laurifolia*); *C. L. Pollard*, May 30, 1896.

NORTH CAROLINA.—New Berne, Craven County, *T. G. Harbison*, June 10, 1917 (nos. 3, 4); Wilmington, New Hanover County, *T. G. Harbison*, June 11, 1917 (no. 110); Abbottsburg, Bladen County, *T. G. Harbison*, May 3, 1916.

SOUTH CAROLINA.—Darlington, Darlington County, *T. G. Harbison*, December 10, 1917 (no. 4); Yemassee, Hampton County, *T. G. Harbison*, December 7, 1917 (no. 1).

GEORGIA.—Lumber City, Telfair County, *T. G. Harbison*, May 30, 1917 (no. 9), December 3, 1917 (no. 11).

FLORIDA.—Jacksonville, Duval County, *T. G. Harbison*, December 3, 1917 (nos. 17, 20); San Mateo, Putnam County, *T. G. Harbison*, December 6, 1917 (no. 36); River Junction, Gadsden County, *T. G. Harbison*, April 19, 1917 (no. 110), November 2, 1917 (nos. 141, 156).

ALABAMA.—Cottondale, Tuscaloosa County, *T. G. Harbison*, May 19, 1917 (no. 38); Mount Vernon, Mobile County, *T. G. Harbison*, May 19, 1917 (no. 16); Cedar Creek, near Selma, Dallas County, *R. S. Cocks*, September 20, 1917; Sardis (now Berlin), Dallas County, *R. S. Cocks*, October 2, 1917 (no. 4706, type).

LOUISIANA.—Slidell, St. Tammany Parish, *R. S. Cocks*, September 30, 1917; Mandeville, St. Tammany Parish, *R. S. Cocks*, September 1914 (no. 4698); Springfield, Livingston Parish, *Cocks* and *Sargent*, March 29, 1917, *R. S. Cocks*, October 3, 1917 (no. 4710); Welsh, Jeff Davis Parish, *E. J. Palmer*, September 1915 (no. 8485); Lake Charles, Calcasieu Parish, *C. S. Sargent*, March 24, 1911; Natchitoches, Natchitoches Parish, *E. J. Palmer*, May 4, 1915 (no. 7500); Monroe, Ouachita Parish, *E. J. Palmer*, October 4, 1915 (no. 8934); Pineville, Rapids Parish, *R. S. Cocks*, October 3, 1917 (no. 4702).

TEXAS.—Beaumont, Jefferson County, *E. J. Palmer*, April 22, 1916 (no. 9524), *C. S. Sargent*, March 23, 1917.

Q. rhombica has usually been confounded with *Q. nigra* L. except in Virginia and Louisiana, where it has passed for *Q. laurifolia* Michx. From *Q. nigra* it differs in the shape of the leaves, in its larger fruit with deeper cups, rounded not flat on the bottom and covered with less closely appressed and less pubescent scales, in its paler bark and more persistent leaves. From *Q. laurifolia* it differs in the shape of its thinner leaves which turn yellow and fall gradually in the early winter, and in its larger fruit with much deeper cups.

QUERCUS RHOMBICA var. **obovatifolia,** n. var.—Differing from the type in the obovate leaves at the ends of the branches, rounded or slightly 3-lobed or undulate at the broad apex.

The terminal leaves of this variety, which are sometimes 10–11 cm. long and 6–7 cm. wide, show a relationship with *Q. nigra* L., but typical *Q. rhombica* leaves occur on the same branches. The texture, color, and venation of all the leaves are those of *Q. rhombica*, and the fruit with a cup 2.5 cm. in diameter is that of that species, as are the winter buds and branchlets.

A single tree in low woods, Beaumont, Jefferson County, Texas, *E. J. Palmer*, September 14, 1917 (no. 1274, type).

QUERCUS LAURIFOLIA Michx.—This is one of the least variable of the southern oaks. The branchlets are always glabrous, and the leaves, which are thicker than those of *Q. Phellos* L., are dark green, very lustrous, and glabrous. On the branches figured by MICHAUX the leaves are generally elliptic, but sometimes slightly broadest above the middle, acuminate at the ends, and 6–12.5 cm. in length. Occasionally trees occur on which lanceolate leaves are found, but in its most common form the leaves of the laurel oak are elliptic and usually not more than 7–8 cm. in length. The leaves of seedlings in their first season are broadly obovate, rounded and 3-toothed or lobed at apex, or are often furnished above the middle with short acute lobes. On leading shoots oblong-obovate leaves acute or rounded at apex sometimes occur, and such leaves are occasionally 3-lobed at apex. When the ends of branchlets have been broken or injured by cattle or horses, summer shoots growing from lateral buds often produce only small narrow oblong leaves irregularly divided into narrow acuminate apiculate lobes, but sometimes at the base of summer shoots the leaves are much larger, oblong-obovate, rounded, and obtusely lobed at apex. Usually the leaves of *Q. laurifolia* are acute at apex, but occasionally obovate leaves rounded at apex are found among leaves of normal shape; and on some individual trees all the leaves, although varying much in width, are of this shape. It was for a tree with such leaves that MICHAUX proposed the name of

QUERCUS LAURIFOLIA (HYBRIDA) Michx. Hist. Chênes Amér. *pl. 18.* 1801.—Differing from the type in its obovate leaves rounded at apex.

MICHAUX, although he suggested that this tree might have been a hybrid between the laurel and water oaks, apparently believed that it was a mere variety of the former, which he says it resembled in all other characters. This variety of the laurel oak, although widely distributed, is not common. It is the only form of the laurel oak which I have seen from Virginia, where it was col-

lected on the banks of the Blackwater River, near Zumi, Isle of Wight County, by *A. Rehder* in August 1908. I have seen specimens from New Berne, North Carolina, where it grows in low woods and where it had been planted as a street tree, from Darlington and Bluffton, South Carolina, and from the banks of the Apalachicola River at Chattahoochee, Florida.

✓QUERCUS LAURIFOLIA var. **tridentata,** n. var.—Differing from the type in its 3-lobed leaves. Leaves oblong-obovate to oblong, gradually narrowed and acute or rounded at base, 3-lobed at apex, often slightly repand below, the terminal lobe acuminate and much larger than the lateral lobes; at maturity thick, glabrous, dark green and lustrous above, paler below, 6–12 cm. long and 2–4 cm. wide, with prominent yellow midribs and primary veins; petioles stout, glabrous, 5–10 mm. in length. Spring leaves and flowers not seen. Fruit as in the type. A large tree with reddish glabrous branchlets, becoming light gray in their second year, and ovate acute puberulous winter buds.

A single tree in a row of planted trees in one of the streets of Orlando, Orange County, Florida, *T. G. Harbison*, December 5, 1917 (no. 26). Three-lobed leaves occasionally occur on vigorous shoots of *Q. laurifolia*, but on this tree all the leaves are 3-lobed and are rather larger than those of the common form of the laurel oak.

As figured by MICHAUX, the cup of the fruit of *Q. laurifolia* is shallow cup-shaped, with rather large and apparently not very closely appressed scales; more often the cup is saucer-shaped and only slightly rounded on the bottom with small closely appressed slightly pubescent scales.

Q. laurifolia, which is one of the most magnificent of the American oaks, is chiefly confined to the coast region, where it is found from Virginia to southern Florida and along the Gulf coast to Mississippi. It is common in the interior of the Florida peninsula, and is not rare in the southern counties of Georgia. From further inland I have seen specimens from Darlington, Darlington County, South Carolina, from the neighborhood of Augusta, Richmond County, Georgia, and from Tuskegee, Macon County, Alabama, but these may have been from planted trees, as the laurel oak has long been a popular street and shade tree in the southeastern states. The laurel oak is not evergreen. Late in the winter the leaves begin gradually to turn yellow and then brown, and when the buds begin to swell at the appearance of spring drop almost simultaneously, leaving the branches bare for a week or two, when they are again covered with unfolding leaves.

QUERCUS CINEREA Michx.—The influence of soil conditions on the growth of trees is well shown by this oak. On dry and sterile

sand hills it is rarely more than 10 m. tall and usually much smaller, with a short trunk and rigid erect branches which form a rather open and unsymmetrical head, but in the richer moist soil of the flats covered by pine woods in the center of the Florida peninsula it is often a tree 20–25 m. high. with a tall trunk and a wide head of gracefully drooping branches. The leaves of *Q. cinerea* are usually entire, but on the ends of branches of occasional trees leaves occur which are oblong-obovate and more or less lobed at the acute or rounded apex, or are divided into short lateral acuminate lobes. This form has been described as

QUERCUS CINEREA β DENTATO-LOBATA A. DC. Prodr. **16**[2]:73. 1864.

Specimens of such leaves I have seen only from Lumber City and Climax, Georgia, San Mateo and Orlando, Florida, and from Cottondale and Mount Vernon, Alabama, where they were collected in May and November 1917 by *T. G. Harbison;* from Chestnut, Natchitoches Parish, Louisiana (*Palmer* no. 9471); and from San Augustine, San Augustine County (*Palmer* no. 9511), and Bryan, Brazos County, Texas (*Palmer* no. 10747).

QUERCUS ALBA L.—There are three varieties of the eastern white oak.

1. The tree with leaves deeply divided, sometimes nearly to the midrib, into narrow lobes lanceolate or obovate and often toothed at apex, and sessile or long-stalked fruit, the scales of the cup being often much thickened. This is the *Q. alba* of LINNAEUS, his "Quercus foliis oblique pinnatifidis: sinubus angulisque obtusis," as he quotes CATESBY's description and figure which represents this form with deeply divided leaves. It is the *Q. alba pinnatifida* of MICHAUX (Hist. Chênes Amér. *pl. 3. fig. 1.* 1801), who considered it the type, as did MICHAUX fils; and it is this form, although it has been usually treated as a variety in recent years, which must be considered the type of the species.

2. The tree with leaves less deeply divided, with broad rounded lobes and usually smaller generally sessile fruit. This form appears to have been first figured by DU ROI in 1772 in his Harbk. Baumz. *pl. 5. fig. 1.* It is the *Q. alba* of ABBOTT and SMITH (Insects of Georgia, *pl. 85*) and of EMERSON's Trees of Massachusetts; and it is this form which later authors have usually considered to be the type of the white oak. This variety may be distinguished as

QUERCUS ALBA var. **latiloba,** n. var.—Differing from the type in its leaves less deeply divided into broad rounded lobes and in its usually smaller fruit.

3. The tree with obovate leaves with margins undulate or slightly lobed with broad rounded lobes. This is the *Q. alba* (*repanda*) of MICHAUX (Hist. Chênes Amér. *pl. 5. fig. 2.* 1801). According to MICHAUX this form of the white oak was common in his time in the Carolina forests, but I have never seen but one tree, and this is growing by the side of the road between Springfield and Ponchatoula in Tangipahoa Parish, Louisiana, where Professor COCKS and I found it on March 29, 1917, just as the staminate flowers were falling and when the tree was very conspicuous from the thick coat of silvery white tomentum which covered the lower surface of the half-grown leaves. COCKS collected fruiting specimens from this tree on October 3, 1917, when the leaves were glabrous, rounded at apex, undulate or slightly divided on the margins into short broad rounded lobes. The fruit is raised on a peduncle 1 cm. long and is 2.5 cm. in length, with unusually thickened turbinate cup-scales. A specimen ex herb. H. A. Gleason, without fruit, on which some of the leaves were of this form, was collected by *G. P. Clinton* at Herod, Illinois, in April 1898.

QUERCUS AUSTRINA Small, Fl. Southeastern U.S. 353. 1903.—In the original description of this tree it is said to attain a height of 15 m., with a trunk diameter of about 1 m. The bark is described as rough and the leaves as "whitish tomentulose but soon becoming glabrous and more or less glaucous beneath." River banks, Georgia and Alabama, are given for the range.

It is probable that this description of the young leaves was made from a specimen of *Q. Durandii* Buckl., which often grows with *Q. austrina*, for the young leaves of *Q. Durandii* are white-tomentulose on the lower surface, while those of *Q. austrina* are always green and glabrous. Trees of *Q. austrina* are often 20–25 m. and occasionally 30–35 m. high, with trunks 1 m. in diameter. It ranges from the coast of South Carolina to western Florida, central Alabama, and central Mississippi, and although not generally distributed is not rare. The earliest specimens which I have seen were collected at Bluffton, South Carolina, in 1883 by MELLICHAMP, who considered it a hybrid.

It has been suggested (ASHE in Proc. Soc. Am. Foresters **11**:89) that this is the *Q. sinuata* Walter (Fl. Car. 235), the leaves of which were described as

"supra pallidis, subtus subglaucis," but as the leaves of *Q. austrina* are bright green on both surfaces, WALTER'S *Q. sinuata* was probably not that species. The description of the leaves would better apply to *Q. Durandii* Buckl., although the leaves of that species are not "supra pallidis," but, "subplanis" might be used to describe the very shallow cups. *Q. Durandii*, however, is not known to grow in Carolina or nearer Charleston than Albany, Georgia, which so far as I know is the eastern station for this oak, and it is hardly safe to take up WALTER'S name for *Q. Durandii*, especially as his specimen is not found in his herbarium in the British Museum.

QUERCUS STELLATA Wang.—That the post oak should have developed many forms is not surprising, for it is distributed from southern Massachusetts to western Oklahoma and to western Texas, and is found on dry hillsides, sandy plains, and deep bottom lands often inundated for several weeks at a time. Except in size, the fruit of *Q. stellata* shows little variation, and the leaves, which vary greatly in shape and in the character of their pubescence, cannot be depended upon to separate the different forms. On what is considered the typical post oak the upper lateral lobes of the leaves are broad and truncate or slightly lobed at apex. On trees with leaves of this shape leaves are often found with the upper lobes narrowed and rounded at apex; and the clusters of fascicled hairs on the upper surface, which usually well distinguish through the season the northern or typical form of this tree, are often early deciduous or entirely wanting from other forms. On the northern tree the branchlets of the year are stout and thickly covered with pale tomentum, and on some of the southern forms the branches are more slender and glabrous or only slightly pubescent when they first appear, and in the branchlets is the best character I have found by which to group the different forms. The pubescence on the lower surface of the leaves of forms with glabrous branchlets is usually loose or floccose and sometimes deciduous. The close pubescence of fascicled hairs, however, found on the lower surface of the leaves of the typical post oak, is found also on some of the forms with the glabrous branchlets. Forms of the post oak with scaly bark, like that of the white oak, have always with one exception, so far as I have been able to observe, glabrous branchlets and occur only in the south, and the forms on which all or nearly all of the leaves have rounded lobes are also southern.

In the woods 12 miles west of Opelousas, Louisiana, in wet, often inundated ground, there are large post oaks with square lobed leaves glabrous on the upper surface in April, tomentose branchlets, and pale scaly bark. These trees most resemble, except in their bark, the typical post oak, but there is not now sufficient material available to make it possible to treat them as a variety. The following varieties with tomentose branchlets can be distinguished:

QUERCUS STELLATA var. **Boyntonii,** n. var.—*Q. Boyntonii* Beadle, Bilt. Bot. Studies 1:47. 1901.—Differing from the type in the shape of its obovate leaves mostly 3–5-lobed toward the apex with small rounded lobes, and in their yellowish brown pubescence. The leaves are oblong-obovate, gradually narrowed and cuneate or rarely rounded at base, and 3–5-lobed above the middle with broad rounded lobes; when they unfold they are stellate-pubescent above and tomentose below with a thick coat of rusty brown stellate hairs, and at maturity are subcoriaceous, dark green, lustrous and glabrous on the upper surface, tomentose on the lower surface, 9–12 cm. long and 4–7 cm. wide; petioles pubescent, 5–10 cm. in length. The cups of the fruit vary from cup shape to turbinate and their scales are thin and sometimes much thickened toward the base of the cup and are hoary tomentose.

A shrub or small tree spreading into thickets, 1–5 m. tall, with stems covered with rough dark gray furrowed bark, gray-brown branches, and branchlets coated during their first season with yellowish brown tomentum, and glabrous or slightly pubescent in their second season. In the shelter of narrow glades on the summit of Lookout Mountain above Gadsden and Attala, Etowah County, Alabama.

The dwarf habit of this little oak is due probably to the exposed position and high altitude where it grows. It is best distinguished from other forms of dwarf post oaks by the color of the yellow-brown pubescence on the leaves and branchlets, for the fruit is not different from that of the typical post oak, and the shape of the leaves is similar to that of many post oak leaves with rounded lobes.

QUERCUS STELLATA var. **attenuata,** n. var.—Differing from the type in the oblong to oblong-obovate narrow leaves 3-lobed at the apex with small, usually rounded lobes, the lateral rarely truncate at the apex, below slightly undulate or lobed with one or with two small lobes and gradually narrowed to the cuneate base;

at maturity glabrous, smooth or scabrate above and thickly coated below with pale pubescence, 8–14 cm. long and 3–4.5 cm. wide across the terminal lobes; petioles slightly pubescent, 1–1.5 cm. in length; spring leaves and flowers not seen. Fruit nearly sessile; acorn not more than 1.5 cm. long and inclosed for half its length in the turbinate cup 1–1.5 cm. in diameter. A tree with stout tomentose branchlets.

Arkansas Post on the White River, Arkansas County, Arkansas, *John H. Kellogg*, September 24, 1909. Judging by the number of specimens made by *Kellogg*, this must be a common tree at Arkansas Post. Unfortunately I have no notes on its size or the nature of the bark. The leaves resemble in shape those of var. *paludosa*, but the pubescence on the lower surface is not so dense, and the tomentose branchlets distinguish it from that variety.

QUERCUS STELLATA var. **parviloba,** n. var.—Differing from the type in the smaller lobes of the leaves and in their more prominent reticulate veinlets. Leaves obovate to oblong, acute or rounded at the narrow apex, cuneate or rounded at base, 3-lobed at apex or 5-lobed, with small rounded or acute lobes, or nearly entire with undulate margins; at maturity pubescent above, floccose-tomentose below, 6–8 cm. long and 2.5–4 cm. wide, with prominent pubescent midribs and conspicuous reticulate veinlets, or on vigorous shoots sometimes 9–10 cm. long and 4–6 cm. wide; petioles stout, rusty-tomentose, 5–8 mm. in length. Flowers and spring leaves not seen. Fruit as in the species.

A round-headed tree 8–10 m. high, with rough bark and stout branchlets covered with thick rusty brown tomentum during their first season, becoming darker colored and slightly tomentose during the following year, and globose terminal buds.

Dry sandstone hills near Brownwood, Brown County, Texas, *E. J. Palmer*, October 23, 1916 (no. 11105, type); sometimes planted as a street tree in Brownwood.

QUERCUS STELLATA var. **anomala,** n. var.—Differing from the type in its broadly obovate leaves, slightly 3-lobed and rounded at the apex. Leaves 4.5–7 cm. in length and 2.5–3.5 cm. in width, rounded and slightly 3-lobed at apex with broad rounded lobes and entire or undulate and gradually narrowed below to a rounded base; subcoriaceous, lustrous and glabrous above in autumn and tomentose below with a thick coat of fascicled hairs,

with prominent midribs and with the upper primary veins running to the points of the lobes larger than the others; petioles pubescent, 3–4 mm. in length. Flowers and spring leaves not seen. Cup of the fruit turbinate, 1–1.5 cm. in diameter, with scales not at all thickened, loosely appressed; nut not seen.

A tree 5–6 m. tall, with thick bark deeply divided into broad ridges covered with closely appressed scales, stout gray branches, branchlets thickly covered during their first season with rusty tomentum, and ovate obtuse pubescent buds.

Dry sandstone hills, Brownwood, Brownwood County, Texas, *E. J. Palmer*, October 18, 1917 (no. 13037, type), May 14, 1907 (no. 11906).

In the shape of the leaves this is the most abnormal of the forms of the post oak which I have seen and, as PALMER suggests, it may possibly be a hybrid between *Q. annulata* and *Q. stellata* which grow with it.

QUERCUS STELLATA var. **Palmeri,** nov. var.—Differing from the type in its narrow oblong or slightly obovate 5–7-lobed leaves with narrow lobes, in the dense tomentum on their lower surface, and in the thicker more closely appressed tomentose scales of the turbinate cup. The leaves are deeply divided by wide sinuses into narrow acute or rounded, or rarely obliquely truncate lobes and are obtusely pointed at apex, rounded at base, pubescent on the upper surface, coated below with a thick coat of pale tomentum of fascicled hairs, 8–9 cm. long and 3–5 cm. wide; petioles tomentose, 5–8 mm. in length. Flowers and spring leaves not seen. Fruit sessile or short-pedunculate, the cup turbinate with the lower scales often much thickened, and 1.2–1.8 cm. in diameter.

A shrub 2–3.5 m. high, with scaly bark, forming large clumps by underground stems, the tallest specimens in the center of the clump, the smallest near its margins.

Sandy uplands, Elk City, Beckham County, Oklahoma, *E. J. Palmer*, July 16, 1917 (nos. 12564, 13070, type).

QUERCUS STELLATA var. **rufescens,** n. var.—Differing from the type in the rusty brown pubescence on the lower surface of the polymorphous leaves and on the branchlets, in the deeper cups of the fruit, and in their thicker basal scales. The leaves are pubescent above throughout the season and thickly covered with close rusty brown pubescence on the lower surface. They are 5–6 cm. long, 1–1.5 cm. wide, rounded or acute at apex, rounded or

cuneate at base, slightly or deeply lobed with 2–4 pairs of rounded lobes, or undulate or rarely entire; on vigorous shoots they are oblong-obovate with the broad upper lobes of the leaves of the post oak, 6–7 cm. long and 3.5–4 cm. wide; petioles densely pubescent, 4–5 mm. in length. Leaves collected in the spring and flowers not seen. Leaves on some individuals oblong-obovate, broad or gradually narrowed and rounded at apex, cuneate at base, slightly divided into two or three pairs of broad rounded lobes, 5–7.5 cm. long and 3.5–4.5 cm. wide; on others oblong-obovate, 7-lobed, the lateral lobes of the upper pair rounded or truncate at apex, or occasionally 5-lobed, the truncate upper lateral lobes like those of the type. Fruit sessile or short-pedunculate; cup turbinate, rusty pubescent, the lower scales often much thickened, inclosing one-half to three-quarters of the nut, and 1.2–1.8 cm. in diameter.

Shrubs 4–5 m. high, with scaly bark, spreading by underground stems into large thickets, and slender branchlets thickly covered during their first two seasons with rusty brown pubescence; rarely small trees.

Sandy uplands, Elk City, Beckham County, western Oklahoma, *E. J. Palmer*, July 16, 1917 (no. 12570, type), October 25, 1917 (no. 13069).

TEXAS.—Big Springs, Howard County, *E. J. Palmer*, July 9 and October 23, 1917 (nos. 12489, 13063, 13064, with oblong-obovate leaves with rounded or truncate upper lobes. "In sandy soil this shrubby post oak grows in large clumps to a maximum height of 4 m.; it suckers freely and is a very conspicuous feature of the flora on account of its peculiar growth, dark green foliage, and greater height among large areas of *Q. Mohreana*)"; Fort Chadburn, Coke County, *E. J. Palmer*, July 7, 1917 (no. 12462, "shrubs or small trees 2–3 m. high"); dry gravel hills, Sweetwater, Nolan County, Texas, *E. J. Palmer*, October 21, 1917 (no. 13054, with narrow slightly lobed or undulate leaves; "a tree 6–8 m. high; branches stout, rigid; bark rough").

The following varieties with glabrous or nearly glabrous branchlets can be distinguished:

QUERCUS STELLATA var. MARGARETTA Sargent in Trees and Shrubs **2**:219. 1913.—*Q. minor* var. *Margaretta* Ashe, Jour. Elisha Mitchell Sci. Soc. **11**:94. 1894; *Q. Margaretta* Small, Fl. Southeastern U.S. 355. 1903.—Differing from the type in the usually rounded lobes of the leaves soon glabrous on the upper surface, in the less dense sometimes nearly deciduous pubescence on the lower surface, and in the slender glabrous reddish branchlets.

This is the common post oak of the south Atlantic and Gulf states, where it grows usually on dry gravelly or sandy slopes and ridges, and is a small tree with close furrowed rough bark. Occasionally the leaves do not differ in shape from those of the typical northern post oak.

QUERCUS STELLATA var. MARGARETTA f. **stolonifera,** n. f.—I suggest this name for a form of this oak which is common near Selma, Dallas County, Alabama, which differs from the variety in habit and in its smaller leaves. It is a shrub usually only 1.5–2 m. high, spreading into thickets by stoloniferous shoots; the branchlets are glabrous or slightly pubescent when they first appear.

C. S. Sargent, April 19, 1915; *T. G. Harbison*, April 20, 1915; *R. S. Cocks* (no. 962, type), September 18, 1915.

It is probably this form which covers the dry sandy hills west of Oklahoma City, Oklahoma, with low dense thickets.

QUERCUS STELLATA var. **araniosa,** n. var.—Differing from the type in the usually smooth upper surface of the leaves, in the floccose persistent tomentum on their lower surface, and in the more slender yellow or reddish usually glabrous branchlets and scaly bark.

LOUISIANA.—Natchitoches Parish, Grand Ecore, *E. J. Palmer* (no. 8770, type), October 2, 1915; also *Palmer*, nos. 7518, 7978, 8769, 8838, 9446; Chopin 7361, 7978, 8838; Natchitoches 7361.

TEXAS.—Larissa, Cherokee County, *E. J. Palmer* (nos. 7840, 8607); Liberty, Liberty County, *E. J. Palmer* (no. 7723, a large tree with slightly scaly bark).

OKLAHOMA.—Antlers, Pushmataha County, *E. J. Palmer* (no. 8318); Broken Bow, McCurtain County, *E. J. Palmer* (no. 10491).

ARKANSAS.—Texarkana, Miller County, *E. J. Palmer* (no. 8985); Benton, Saline County (no. 8439).

ALABAMA.—Common in dry sandy soil near Selma, Dallas County, *R. S. Cocks*, September 15, 1915 (no. 956); *T. G. Harbison*, 1911–1916 (nos. 53, 54).

The leaves of this variety have sometimes square and sometimes rounded lobes, leaves with square and rounded lobes often appearing on the same branch. The fruit is sessile or occasionally raised on peduncles up to 1.6 cm. in length.

QUERCUS STELLATA var. **paludosa,** n. var.—Differing from the type in its oblong-obovate leaves, mostly 3-lobed above the middle, slightly pubescent branchlets sometimes becoming nearly glabrous, and in its scaly bark. Leaves oblong-obovate, gradually narrowed below into a long slightly undulate cuneate base, rarely furnished near the middle on one side, or on each side, with a small rounded

lobe, and 3-lobed toward the apex, the terminal lobe gradually narrowed and rounded at apex or sometimes divided into 3 small rounded terminal lobes, the lateral lobes gradually narrowed, rounded and entire, or broader, nearly truncate and slightly 2-lobed at apex; when they unfold thickly covered above with fascicled hairs and below with thick persistent tawny pubescence; at maturity thick, dark green, lustrous and scabrate on the upper surface, 8–12 cm. long and 4–6 cm. wide across the lobes, with stout midribs and two prominent veins running to the ends of the lobes, and thickened slightly revolute margins; petioles covered when the leaves first appear with pubescence, soon mostly deciduous, and 10–12 mm. in length. Flowers and fruit as in the species.

A tree 20–25 m. tall, with a trunk sometimes 1 m. in diameter, covered with pale bark separating into thin usually appressed scales, stout branches forming a narrow round-topped head, and slender branchlets dark red and sparingly stellate-pubescent when they first appear, and red-brown or gray-brown and slightly pubescent or nearly glabrous later in the season. Winter buds ovate, obtusely pointed, with red-brown pubescent scales.

In deep rich soil on the often inundated bottoms of Kenison Bayou, near Washington, St. Landry Parish, Louisiana, *Cocks* and *Sargent*, March 26, 1917, *R. S. Cocks*, October 12, 1917 (nos. 4730, 4732, 4734, type). At this station there are 8 trees of this distinct variety of the post oak.

QUERCUS MUEHLENBERGII var. **Brayi,** n. var.—*Q. Brayi* Small, Bull. Torr. Bot. Club **28**:358. 1901.—The chestnut oak of western Texas differs from *Q. Muehlenbergii* Englem. only in its larger fruits, which are sometimes 3 cm. long with cups 1.5 cm. deep and 2.5 cm. in diameter, with slightly more thickened scales.

Such fruit is found on trees on the Edwards Plateau where this oak is not rare in low ground in the neighborhood of streams. The type tree is a large specimen on the bottom lands of a small stream at Lacey's Ranch near Kerrville, Kerr County. Farther west the fruit is smaller, and on the Guadalupe Mountains, which is the western known limit of the range of this chestnut oak, the fruit is small, with cups not more than 1.5 cm. in diameter.

QUERCUS UTAHENSIS var. **submollis,** n. var.—*Q. submollis* Rydberg, Bull. N.Y. Bot. Garden **2**:202. 1901.—Differing from the type only in the thinner scales of the cup of the fruit.

Q. submollis as a species was based on the thin scales of the cup of the fruit. The cup-scales of *Quercus* do not, however, afford a valuable character

for distinguishing species, and in the case of *Q. utahensis* trees occur with cups showing a complete gradation between those with much thickened scales and those with only slightly thickened scales. Trees with the thickened and with the thin cup-scales occur over the whole region occupied by the species, but var. *submollis* seems rather more abundant on the Colorado plateau in northern Arizona where *Q. utahensis* and its variety are the largest and most abundant oaks.

QUERCUS ANNULATA Buckley, Proc. Phil. Acad. 1860. 445, is the earliest specific name for this white oak of western Texas, which was first described as *Q. obtusifolia* var. *breviloba* by TORREY in Bot. Mex. Bound. Surv. 206. 1895, and later by me as *Q. breviloba* in Garden and Forest **8**:93. 1895.

Q. annulata grows on the dry limestone hills of central Texas and is a large or small shrub spreading into thickets, or rarely a tree 10–12 m. tall. I formerly united *Q. Durandii* Buckl. with this species. They both grow in the neighborhood of Austin, Texas, but the two trees differ in habit and in distribution, for *Q. annulata* is confined to the dry hills of central and western Texas, while *Q. Durandii* ranges eastward to Mississippi, Alabama, and Georgia, and is a large tree of bottom lands. They are well distinguished, too, by the larger leaves and by the shallower cups of the fruit of *Q. Durandii*. The leaves of these two oaks differ on different parts of the tree; on fertile branches they are usually covered below with pale tomentum; on lower branches and on vigorous shoots they are green and glabrous or nearly glabrous on the lower surface, and sometimes all the leaves are green on the lower surface. *Q. annulata* is the commonest "shin oak" on the Edwards Plateau of Texas, where with bushes 1–2 m. high it covers thousands of acres of dry limestone hills, or in the protection of bluffs and ravines occasionally becomes a tree 8–10 m. tall.

QUERCUS MOHRIANA Rydb.—This species must be added to the list of North American trees, for although usually a shrub not more than 1.5 m. high, *E. J. Palmer* has found it growing as a tree 7–8 m. tall, with a trunk 3 dm. in diameter, in the shelter of bluffs and ravines, Nolan County, Texas.

Q. Mohriana is common on the Staked Plains of Texas, and from Tom Green County northward it replaces *Q. annulata* Buckl. on the slopes and tops of dry calcareous hills.

QUERCUS VIRGINIANA Miller.—The fact that there are two distinct principal forms of the live oak in the southern states appears to have escaped the attention of most authors who have written about this tree. On one of the forms the leaves are comparatively

thin, with only slightly revolute margins and reticulate veins inconspicuous on the lower surface, which is covered with very short close pale pubescence. On the other form the leaves are much thicker, with conspicuously revolute margins and reticulate veins prominent on the lower surface which is covered with thick pale tomentum. The habit of the mature trees of the two forms is the same, and they both have the same dark gray furrowed bark and the same fruit.

At Biloxi, Mississippi, where these two forms are very abundant and grow together near the sandy shore of the Sound, on April 2, 1917, the leaves of the previous year had practically all disappeared from the first variety, the new leaves were nearly fully grown, and the staminate flowers had fallen, while the trees of the second variety still retained all the leaves of the previous season and showed no signs of vegetative activity. The leaves of the thin-leaved form usually show a tendency to undulate on the margins and are often lobed, especially on trees in western Texas, but on the thick-leaved form I have seen few lobed leaves. Occasionally trees of the thin-leaved form occur on which the leaves are thicker than usual, with thicker and more revolute margins, showing a tendency to intergrade with the other form, although usually the two forms appear very distinct. The thin-leaved form is the more widely distributed, and, except in the interior of the Florida peninsula, the more common tree. It is possibly a larger tree than the other; at least all the very large live oaks I have seen are of this variety. Of the thick-leaved form I have seen specimens outside of Florida only from Wrightsville and Southport, North Carolina, Bluffton, St. Helena Island, and Beaufort, South Carolina, Colonel's Island, Coffin County, Georgia, Fish River, Baldwin County, Alabama, and Biloxi, Mississippi. Although very common along the coast of Mississippi it does not, so far as I have observed, cross the Pearl River into Louisiana, and the great live oaks for which that state is famous are all of the other form.

It is not possible to determine precisely which of these two forms is the type of *Q. virginiana* Miller. The first description of this tree, published in 1696, was that of PLUKENET, *Quercus virginiana sempervirens, foliis oblongis sinuatis* and *non sinuatis* (Alm. Bot. 310). This description might apply to either form and equally well to

Q. laurifolia. CATESBY in his Natural History of Carolina describes and figures the live oak, and his specimen, which is preserved in the British Museum and of which Dr. RENDLE has permitted me to see a leaf, is the thin-leaved form. LINNAEUS based his *Q. Phellos* β (Spec. Pl. 994. 1753) on CATESBY's description and figure. There is no doubt therefore about LINNAEUS' plant, which he considered a variety of the willow oak. PHILLIP MILLER in the eighth edition of his Dictionary, published in 1768, first gave the live oak a specific name, *Q. virginiana*. In his description he refers BANNISTER's *Q. sempervirens foliis oblongis non serratis* to his species. This oak, however, is not included in BANNISTER's list of Virginia plants published by RAY, and this quotation may mean that MILLER received from BANNISTER a specimen or seeds with this descriptive phrase. Unfortunately, MILLER's specimen has not been preserved; but as it is possible that his only information in regard to the live oak came from BANNISTER, and as BANNISTER lived in Virginia, where so far as is now known the thick-leaved form does not occur, it is perhaps safe to assume that the type of *Q. virginiana* Miller is the thin-leaved form, that is, the form known to CATESBY and the *Q. Phellos* β of LINNAEUS.

A narrow-leaved shrubby form of the thick-leaved tree growing in the sandy soil of the Florida peninsula has been described by SMALL as *Q. geminata*, and if the thin- and thick-leaved forms of the live oak are considered varieties of one species the name of the thick-leaved tree becomes

✓ QUERCUS VIRGINIANA var. **geminata,** n. var.—*Q. virginiana* Sargent, Silva N.Am. **8**:99 in part, *pl. 395. fig. 3.* 1895; *Q. geminata* Small, Bull. Torr. Bot. Club **24**:438. 1897.—Differing from the type in the more prominently reticulate-venulose leaves hoary-tomentose below, their margins conspicuously thickened and revolute.

SMALL describes the leaves of *Q. geminata* as mostly oblong-elliptic or oblong-obovate. Such shaped leaves are common on Florida specimens, but on the Carolina and Biloxi specimens the leaves are often broadly oblong-obovate and similar in shape to those of some of the common forms of *Q. virginiana*. The statement that the acorns of *Q. geminata* are always in pairs is not borne out in fact, as the fruit on specimens collected by CURTISS near Jacksonville, Florida (2597), is solitary, and on a number of specimens of his also from

Jacksonville there are 3 fruits on the peduncle. The type of *Q. geminata* is described as a shrub or small tree 2–2.5 m. tall, with a trunk diameter of about 15 cm. Many of the Biloxi trees are 20–25 m. tall, with trunks up to 1 m. in diameter. A form of this variety may be distinguished as

QUERCUS VIRGINIANA var. GEMINATA f. **grandifolia,** n. f.—Differing from the variety in its much larger mostly oblong-elliptic leaves. Leaves oblong-elliptic to slightly obovate, acute or rounded at the apex, narrowed and cuneate or rounded at the base, slightly lobed above the middle, pale on the upper surface, tomentose on the lower surface, 10–12 cm. long and 3–5 cm. wide, with thickened revolute margins and conspicuous reticulate veinlets. A tree 10–12 m. high, with stout pubescent or tomentose branchlets.

In low woods in sandy soil. FLORIDA.—Zellwood, Orange County, *T. G. Harbison*, December 4, 1917 (no. 4, type); Apopka, Orange County, *T. G. Harbison*, December 4, 1917; Jacksonville, Duval County, *T. G. Harbison*, December 3, 1917 (no. 13); near Matanzas, St. John County, *T. G. Harbison*, November 4, 1917 (nos. 3, 4); Gainesville, Alachua County, November 11, 1917 (no. 48, with leaves not more than 7 cm. long and 3 cm. wide); San Mateo, Putnam County, *T. G. Harbison*, November 12, 1917 (no. 19); Sumner, Levy County, *T. G. Harbison*, September 25, 1917 (nos. 30, 40, 43).

The following varieties of the thin-leaved or typical *Q. virginiana* can be distinguished:

QUERCUS VIRGINIANA var. **virescens,** n. var.—Differing from the type in the green glabrous or rarely puberulous lower surface of the leaves and in the glabrous branchlets. Leaves thin, elliptic to oblong-obovate, acute or rounded at apex, gradually narrowed and cuneate at base, occasionally slightly undulate or rarely furnished, usually above the middle, with occasionally minute teeth thin (in June), dark green, glabrous and lustrous on the upper surface, green, lustrous, and sparingly and minutely pubescent or glabrous on the lower surface, 7–12 cm. long and 2.5–5 cm. wide, with prominent midribs, slender primary veins, inconspicuous veinlets, and thin margins slightly or not at all revolute; petioles slender, sparingly pubescent, 5–8 mm. in length. Flowers and fruit not seen.

FLORIDA.—A large tree in sandy soil, Gainesville, Alachua County, *T. G. Harbison*, June 17, 1917 (no. 48, type); Sanford, Seminole County, *T. G. Harbison*, May 27, 1917 (no. 1, with a few leaves lobed near the apex; no. 2, with

rather thicker leaves with more revolute margins, 5–8 cm. long and 1.5–3.5 cm. wide); Sumner, Levy County, *T. G. Harbison*, June 28, 1918 (no. 28); Simpson's Hammock, near Little River, Dade County, *C. T. Simpson*, October 1914; four miles west of Long Key, Everglades, Dade County, *E. A. Bessey*, May 1908 (no. 85).

On a specimen of a shoot from Little River the leaves are oblong, acute at apex, rounded at base, acutely lobed, sometimes with three terminal lobes and sometimes with numerous lateral lobes.

QUERCUS VIRGINIANA var. **macrophylla,** n. var.—Differing from the type in its much larger ovate or slightly obovate leaves, rounded or cuneate at base and rounded or acute at apex, entire or occasionally repand-dentate, and coated below with short pale or nearly white tomentum.

Sandy bottoms of the Atascosa River, and in flat woods just above the river, Pleasanton, Atascosa County, Texas, *E. J. Palmer*, September 23, 1916 (no. 1079, type), May 17, 1916 (no. 9784).

In the shape and size of the leaves, which are 7–10 cm. long and 3–6 cm. wide, and borne on stout pubescent petioles 4–5 mm. in length, this tree is unlike any of the forms of the live oak which in its typical form is common on dry hills in the neighborhood. The fruit is solitary or in pairs, and is borne on peduncles which are 1–5 cm. in length. PALMER reports that there are a number of good sized trees in these groves.

QUERCUS VIRGINIANA var. **eximia,** n. var.—Differing from the type in its narrow elliptic to narrow oblong-obovate leaves, in its smaller size and pale bark. Leaves narrow elliptic to narrow oblong-obovate, abruptly or gradually narrowed and apiculate at the acute apex, gradually narrowed and cuneate at base, on vigorous shoots sometimes lobed on each side near the base, and occasionally near the apex with small acute lobes; when they unfold sparingly pubescent above and thickly covered below with hoary pubescence, and at maturity dark green, lustrous and glabrous on the upper surface, covered on the lower surface with matted pale hairs, 3–5 cm. long and 1–2 cm. wide, with only slightly revolute margins and inconspicuous veins; petioles pubescent, 4–5 mm. in length. Flowers like those of the species; fruit usually smaller with nuts not often more than 1 cm. long and cups 1.2–1.5 cm. in diameter.

A tree 5–7 m. high, with a short trunk 20–30 cm. in diameter covered with pale only slightly furrowed bark, pendulous branches forming a round-topped

head, and slender branchlets covered when they first appear with fascicled hairs and glabrous or nearly glabrous in the autumn; often a shrub not more than 2 m. tall.

In dry sandy open woods, eastern Louisiana, near Springfield, Livingston Parish, *R. S. Cocks* and *C. S. Sargent*, March 27, 1917, *R. S. Cocks*, October 2, 1917 (no. 4716, type); near Hammond, Tangipahoa Parish, *R. S. Cocks*, October 2, 1917 (nos. 4720, 4726, shrubs); Pearl River, *R. S. Cocks*, October 2, 1917 (nos. 4718, 4722, shrubs).

In the texture of the leaves and their slightly revolute margins and inconspicuous veins this variety resembles what is here considered the typical *Q. virginiana*, from which it differs in the small size of the leaves and fruit, in the pale nearly smooth bark, in the more glabrous branchlets, and in its smaller size. So far as I know, this variety has been found only at a few stations in eastern Louisiana and probably is not common.

QUERCUS VIRGINIANA var. **fusiformis,** n. var.—*Q. fusiformis* Small, Bull. Torr. Bot. Club **23**:357. 1901.—Differing from the type in its smaller leaves and smaller size. The leaves are oblong to oblong-obovate, acute at apex, rounded or cuneate at base, entire, or occasionally dentate above the middle, coated below with pale pubescence, 2–2.5 cm. long and 8–10 mm. wide, with slightly thickened and revolute margins. Fruit smaller than in the type and as often short-oblong as fusiform.

A shrub 1–4 m. high, with ridged horizontal or slightly ascending branchlets densely tomentose or pubescent in their first season.

Dry limestone ridges and flat topped hills of the Edwards Plateau, Texas; Lacey's Ranch, near Kerrville, Kerr County, *E. J. Palmer*, June 10, 1917 (no. 12224); "Devil's Back Bone," near Fischer's Store, Coval County, *E. J. Palmer*, June 6, 1917 (no. 12202).

This little live oak grows always in the neighborhood of larger trees of *Q. virginiana*, which it resembles in everything but in its dwarf habit and small leaves, due probably to the exposed and dry situation where it grows.

Sargent, nov. comb.

QUERCUS VIRGINIANA var. DENTATA ~~Chapman, Fl. 421.~~ 1861.—*Q. virginiana* var. *minima* Sargent, Silva N.Am. **8**:101, *pl. 396*. 1895; *Q. minima* Small, Bull. Torr. Bot. Club **24**:438. 1897.—This little oak, which is common in sterile pine barrens near the Florida coast and often bears large crops of fruit when not more than 3 dm. high, is distinct in the lower leaves, which are oblong-obovate, acute at the broad apex, coarsely repand-dentate with large triangular teeth, 7–10 cm. long and 2–3 cm. wide, the upper leaves

being oblong-lanceolate and entire. The fruit is usually larger, with shorter peduncles than on large trees.

QUERCUS VIRGINIANA var. MARITIMA Sargent, Silva N.Am. 9:100. 1895.—*Q. virens* (*maritima*) Michx. Hist. Chênes Amér., No. 7, *pl. 13. fig. 3.* 1801; *Q. virens* var. *maritima* Chapman, Fl. 421. 1860.—Leaves oblong-obovate to rarely lanceolate, acute and apiculate or rounded at apex, gradually narrowed and cuneate at base, entire or slightly and irregularly toothed above the middle, 5–8 cm. long and 1–1.5 cm. wide. Fruit solitary or in pairs, on peduncles 1–5 cm. in length. A shrub often not more than 2 dm. tall.

Dry sandy barrens, coast of South Carolina to Miami, Dade County, Florida. *Q. succulenta* Small (Fl. Southeastern U.S. ed. 2, 1332) from Dade County, Florida, appears to be a form of the var. *maritima* with the fruit in elongated spikes.

QUERCUS VIRGINIANA var. PYGMAEA, n. var.—Differing from the type in the usually 3-lobed leaves and in its smaller size. Leaves oblong-ovate, gradually narrowed and cuneate at the entire base, 3- or occasionally 5-lobed at apex with small acute lobes, or rarely elliptic and entire, glabrous on the upper surface, slightly pubescent at maturity on the lower surface, 3.5–6 cm. long and 2–2.5 cm. wide, with thin slightly revolute margins and inconspicuous veinlets; petioles 4–5 mm. in length, pubescent. Fruit nearly sessile or raised on short peduncles, the nut 1–1.5 cm. long and inclosed nearly to the apex. A shrub rarely more than 1 m. tall, with reddish brown stems and puberulous branchlets.

FLORIDA.—Pine woods in sandy soil, Zellwood, Orange County, *C. H. Baker*, August 1915 (type); dry river banks near Jacksonville, Duval County, *A. H. Curtiss*, November 1893 (without number); Sanford, Seminole County, *C. S. Sargent*, April 4, 1886; Sopchoppy, Wakulla County, *W. M. Canby*, April 3, 1895; vicinity of Fort Myers, Lee County, *Jeanette P. Standley*, June 26, 1916 (no. 289, with smaller thin leaves hoary-tomentose on the lower surface; perhaps another form).

GEORGIA.—Sandy soil near the coast, Brunswick, Glynn County, *T. G. Harbison*, November 3, 1913 (no. 32, with smaller fruit and shallower cups).

This variety appears to have been usually confused with var. *dentata*, but from that variety it differs in the absence of the large, many lobed leaves at the base of the stems and in the smaller fruit.

In the central peninsula of Florida, especially after the forest floor has been burned, small plants of the thick-leaved live oak spread by underground stems into large thickets of small stems which often bear lanceolate or narrow obovate leaves acute or rounded at apex and entire or irregularly toothed with small apiculate teeth. Some of these stems survive for many years and form a ring of smaller trees around the large central tree. The small plants in these clusters rarely produce fruit. In western Texas the live oak often spreads also by underground stems and forms clusters of considerable size.

An abnormal shrubby form of the live oak, with fruit in many fruited spikes 9–10 cm. long was collected by G. V. NASH in the vicinity of Eustis Lake, Lake County, Florida, April 1894 (no. 1762) and was distributed under the name of *Quercus virens spicata* Chapman. This name does not appear to have been published, and I have seen no other specimens like this no. 1762.

HYBRID OAKS

Quercus Hastingsii, n. hyb. (*Q. marilandica* × *texana*).—Leaves broadly obovate to ovate, rounded or abruptly cuneate at the wide base, 5-lobed halfway to the midrib by usually wide sinuses rounded in the bottom, the terminal lobe oblong, slightly 3-lobed at apex, the upper lateral lobes wide and slightly 2-lobed or rounded and entire at apex, more than twice as large as the entire rounded or acute lower lobes; at maturity thin, lustrous and glabrous on the upper surface, paler and glabrous on the lower surface, 6–7 cm. long and 5–6 cm. wide, with pubescent midribs and conspicuous axillary tufts of pale hairs; petioles slender, pubescent, 10–12 mm. in length. Flowers and spring leaves not seen. Cup of the fruit turbinate, covered with broad loosely appressed scales, gradually narrowed and rounded at apex and hoary-tomentose except on the margins, those of the upper rank conspicuously ciliate; fruit not seen.

A tree with a trunk 20 cm. in diameter, with branchlets thickly coated during the first season, with close pale tomentum, and small ovate pubescent winter buds.

TEXAS.—Near Boerne, Kendall County, *S. H. Hastings*, October 1910 (type); Woods along small creek, Brownwood, Brown County, *E. J. Palmer*, October 18, 1917 (no. 13056, with branchlets becoming nearly glabrous).

In shape the leaves of this tree differ from those of *Q. texana* in the shallower sinuses and in the less deeply divided terminal lobe, but, with the exception of the pubescence along the midribs and on the veins, most resemble the leaves of that species although they have conspicuous axillary tufts. The influence of *Q. marilandica* is seen in the broad tomentose scales of the cup, in the tomentose branchlets, and in the short tomentose winter buds.

I take much pleasure in associating with this interesting tree the name of its discoverer, S. H. HASTINGS, for many years at the head of the United States Agricultural Experiment Station at San Antonio, Texas.

Quercus beaumontiana, n. hyb. (*Q. rhombica*×*rubra*).—Leaves rhombic to oblong or oblong-obovate, acute at the ends, entire or undulate, and at the ends of the branchlets, deeply 3-lobed at apex with acuminate lobes and undulate and occasionally slightly lobed below; at maturity thin, smooth, and glabrous on the upper surface, sparingly pubescent on the lower surface, those with undulate or obscurely lobed margins 7–8 cm. long and 3–4 cm. wide, the terminal lobed leaves 9–12 cm. long and 5–7 cm. wide across the lobes; petioles slender, glabrous, 1–2.5 cm. in length. The fruit is that of *Q. rhombica*.

A tree with glabrous branchlets and oblong-ovate glabrous winter buds.

A single tree growing in a row of trees on a street leading out to Magnolia Cemetery, Beaumont, Jefferson County, Texas, and probably transplanted from woods in the neighborhood, *E. J. Palmer* (no. 12748, type). Another tree growing on a street west of Beaumont with undulate leaves coated below with pale pubescence as they unfold and glabrous branchlets is possibly the same hybrid (*C. S. Sargent*, April 11, 1915).

QUERCUS MELLICHAMPII Trelease, Proc. Am. Phil. Soc. **56**:50. 1917 (*Q. Catesbaei*×*laurifolia*) (nomen nudum).—To an oak which was found many years ago on a sandy ridge by *J. H. Mellichamp* near Bluffton, South Carolina (see SARGENT, Silva N.Am. **8**:144. *pl. 419*), TRELEASE has given the name of its discoverer. This oak, as ENGELMANN pointed out long ago, has every evidence of being a hybrid between *Q. Catesbaei* Michx. and *Q. laurifolia* Michx.

Trees which are evidently the result of the same cross are not rare in San Mateo, Putnam County, Florida, and in the neighborhood of Orlando, Orange County, Florida, where several trees of this hybrid growing in the woods in

dry sandy soil sometimes reach a height of 20 m. and form trunks 40–50 cm. in diameter, covered below with nearly black deeply furrowed bark. In the neighborhood of Orlando this tree is called silver oak from the pale color of the smooth upper stem and large branches. On the Florida trees sometimes occur lanceolate or oblong-elliptic entire leaves which I have not seen on the specimens collected near Bluffton by MELLICHAMP. In Florida the leaves of these trees begin to fall in December and fall gradually during the winter. My attention was first called to the silver oak in April 1915 by C. H. BAKER of Zellwood, near Orlando. It has been since collected in Orange County and in the neighborhood of San Mateo by *T. G. Harbison* and myself.

QUERCUS DUBIA Ashe, Jour. Elisha Mitchell Sci. Soc. **11**:93. 1894.—*Q. atlantica* Ashe, Proc. Soc. Am. Foresters **11**:88. 1916; *Q. sublaurifolia* Trelease, Proc. Am. Phil. Soc. **56**:52 (nomen nudum). 1917; (*Q. cinerea*×*laurifolia*).—The specimens which I believe represent this hybrid all have rather thick leaves pubescent on the lower surface and pubescent branchlets. The leaves vary greatly in shape and size; those of the type of *Q. dubia* from Abbotsford, Bladen County, North Carolina, are oblong, acute at apex, unsymmetrical and rounded at base, sometimes slightly falcate, 14–16 cm. long and 5.5–7.5 cm. wide. Specimens with similar leaves were collected at Jacksonville, Florida, by A. H. CURTISS many years ago. Unfortunately these specimens are not numbered or dated. He considered them a large-leaved form of *Q. laurifolia*. The type of *Q. atlantica* collected by *Ashe* at Lumber City in southern Georgia has many of the leaves obovate and rounded at apex and others elliptic or lanceolate and acute, resembling in size and shape those of *Q. laurifolia* and sometimes, like those of that species, they are slightly lobed toward the apex. The fruit of this hybrid is nearly sessile or distinctly pedunculate. On some trees it has the shallow cups of *Q. laurifolia* and on others cups as deep and broad as those of the large fruited forms of *Q. cinerea*. The trees of this oak which I have seen in Florida were not more than 12 m. high, with trunks 35–40 cm. in diameter, covered with dark deeply furrowed bark resembling that of *Q. cinerea* and with stiff erect branches forming an open head.

In addition to the specimens collected by CURTISS and ASHE I have seen specimens which seemed to belong to this hybrid collected by T. G. HARBISON in 1917 at Abbottsburg, Bladen County, North Carolina; Saint Helena Island

and Port Royal, Beaufort County, South Carolina; Lumber City, Telfair County, and Climax, Decatur County, Georgia; Jacksonville, Duval County, Gainesville, Alachua County, San Mateo, Putnam County, Zellwood, Orange County, Lake City, Columbia County, Florida; and from Mississippi City, Lincoln County, Mississippi.

Quercus Bushii, n. hyb. (*Q. marilandica*×*velutina*).—Leaves broadly obovate, rounded or rarely acute at base, 5-lobed with broad acute conspicuously apiculate lobes, the lobes of the lower pair much smaller than the others, or sometimes 3-lobed, the terminal lobe entire or sometimes minutely 3-lobed at apex; at maturity thick, dark green, lustrous and glabrous on the upper surface, yellowish brown and glabrous with the exception of a slight pubescence on the lower side of the midribs, 10–12 cm. long and 6–10 cm. wide, the veins running to the points of the lobes much larger than the others; petioles stout, floccose-pubescent, becoming nearly glabrous, 1–1.5 cm. in length. Flowers and spring leaves not seen. Fruit sessile, the nut ovate, rounded at the broad apex, finally becoming nearly glabrous, inclosed for one-half to nearly two-thirds of its length in the turbinate cup; cup-scales loosely appressed, broad and rounded at apex, hoary-pubescent, those of the upper ranks ciliate at the apex.

A tree with stout pale pubescent or in the autumn nearly glabrous branchlets and ovate acuminate narrow winter buds, the scales of the outer ranks covered with pale or rufous silky pubescence.

Oklahoma.—Sapulpa, Creek County, *B. F. Bush*, September 20, 1895 (no. 1328, type).

Mississippi.—Oxford, Lafayette County, *T. G. Harbison*, October 16, 1915 (no. 16, with larger leaves 5 or rarely 7-lobed, and larger fruit).

Alabama.—Dothan, Houston County, *T. G. Harbison*, May 23, 1917 (no. 8, a small tree); near Berlin, Dallas County, *R. S. Cocks* (no. 1002); bank of Mobile Bay at Daphne, Baldwin County, *C. S. Sargent*, October 14, 1913. A large tree with pendulous branches, nearly glabrous branchlets, and pubescent winter buds, close dark bark and shallower cups than those of the Oklahoma tree. The leaves on the fertile branchlets of this tree are 3-lobed, but at the ends of vigorous shoots they are narrow-obovate to oblong and are slightly divided into 3 or 4 pairs of lateral lobes. Mount Vernon, Mobile County, *T. G. Harbison*, May 19, 1917 (no. 21, without fruit and possibly a hybrid between *Q. Catesbaei* and *Q. marilandica*).

FLORIDA.—Sumner, Levy County, *T. G. Harbison*, June 16, 1917 (no. 3 A, "medium-sized tree in low hammocks").

GEORGIA.—Climax, Decatur County, *T. G. Harbison*, November 6, 1917 (no. 7).

QUERCUS SUBFALCATA Trelease, var. **microcarpa,** n. hyb. (*Q. Phellos*×*rubra ?*).—Leaves oblong-lanceolate to oblong-obovate, acuminate at the ends, slightly divided into numerous small acuminate lateral apiculate lobes, glabrous above, coated below with close pale pubescence, often becoming glabrous late in the season, 7–9 cm. long and 1.5–2 cm. wide; petioles slender, tomentose, sometimes becoming nearly glabrous late in the season. Fruit solitary or in pairs, short-stalked, 1 cm. long, with a shallow turbinate cup with closely appressed pubescent scales rounded at apex, and inclosing about one-third of the ovate acute pubescent nut.

A small tree with slender reddish branchlets thickly coated early in the season with pale tomentum, becoming glabrous in the autumn, and small ovate acute glabrous winter buds.

The parentage and history of this oak are not clear. There can be little doubt, however, that it owes its narrow leaves to *Q. Phellos*, and no other oak but *Q. rubra* L. could produce a hybrid hardy in Massachusetts with the pale pubescence of this plant.

This oak was obtained by the Arnold Arboretum in 1903 from the Wezelenberg Nurseries at Hazerswoude, Holland, under the name of *Q. chinensis microcarpa,* and is now well established here, having begun to produce fruit in 1909.

In September 1913 I found what seems to be the same plant growing in a bed of seedlings said to be *Q. coccinea* planted by Mr. C. S. MANN in his garden at Hatboro, Pennsylvania.

Q. subfalcata (*Q. Phellos*×*rubra*) Trelease has much larger, less lobed, and less pubescent leaves, and larger fruit, and is a native of southern Arkansas and eastern Texas.

Quercus guadalupensis, n. hyb. (*Q. macrocarpa*×*stellata*).—Leaves oblong-obovate, rounded at apex, gradually narrowed and rounded at base, 5- or rarely 7-lobed, the lateral lobes rounded or broad and truncate at apex; at maturity thin, bluish green, smooth and glabrous on the upper surface, coated below with loose pubescence, 8–10 cm. long and 4.5–6 cm. wide, with prominent pubescent midribs; petioles pubescent, 8–10 mm. in length. Spring leaves and flowers not seen. Fruit solitary, sessile or short-pedunculate,

the nut ovate, gradually narrowed and rounded at apex, puberulous, 2.5–3 cm. long and 2 cm. in diameter, and inclosed for one-third of its length in the cup-shaped cup covered with acuminate hoary-tomentose scales, those of the upper ranks forming a ciliate marginal ring.

A tree with stout branchlets covered during their first season with rusty brown tomentum, becoming gray and glabrous the following year, and ovate acuminate puberulous winter buds.

On a rocky creek bank at Fredericksburg Junction in the valley of the upper Guadalupe River, Kendall County, Texas, *E. J. Palmer*, October 1, 1916 (no. 10878, type).

In shape and size the leaves of this tree are intermediate between those of its supposed parents; the pubescence on their lower surface is that of *Q. stellata*. The fruit in size resembles that of *Q. macrocarpa*, but the scales of the cup are less acuminate than those of that species, and the marginal fringe of the cup is only slightly developed. The tomentum of the branchlets is that of *Q. macrocarpa*.

Quercus Andrewsii, n. hyb. (*Q. macrocarpa*×*undulata*).—Leaves oblong-obovate, acute or rounded at apex, rounded at base, divided into 7 or 9 narrow acute or rounded lobes by narrow sinuses rounded in the bottom and extending sometimes halfway to the midrib; at maturity light green and scabrate by the remains of clusters of fascicled hairs on the upper surface, paler and floccose pubescent on the lower surface, 9–12 cm. long and 4.5–6 cm. wide; petioles stout, pubescent, 10–12 mm. in length. Flowers and spring leaves not seen. Nut ovate, narrowed, rounded and depressed at apex, covered with short pale pubescence, 2.5 cm. long, 1.8 cm. in diameter, the cup turbinate with acute hoary-tomentose scales thickened on the back, those of the upper ranks abruptly narrowed into long slender tips forming a marginal ring.

A clump of large shrubs spreading by underground stems. with stout pubescent orange-red branchlets marked by numerous pale lenticels.

Seiling, Dewey County, Oklahoma, growing with its supposed parents. *D. M. Andrews.*

The influence of *Q. macrocarpa* is evident in the lyrate leaves, in the large fruit and its cup-scales, and in the color of the branchlets. The dwarf habit, the underground stems, and the pubescence on the under surface of the leaves show the influence of the other parent. This is one of the most distinct and interesting of the hybrid oaks of North America, and I am glad to associate with it the name of its discoverer, D. M. ANDREWS, of Boulder, Colorado.

Quercus jolonensis, n. hyb. (*Q. Douglasii*×*lobata*).—I suggest this name for a number of large trees at Jolon and between Jolon and King City, Monterey County, California, with characters intermediate between those of *Q. Douglasii* Hook and Arn. and *Q. lobata* Née, with which they are growing and of which they are probably hybrids. They have usually the lobed leaves of *Q. lobata* but are bluish in color, and occasionally one of the entire leaves of *Q. Douglasii* occurs on the specimens. The nuts generally resemble in size and shape those of *Q. lobata*, but occasionally are thickened at the middle like those of *Q. Douglasii*, but the cup is shallow, sometimes saucer-shaped, and the cup-scales are sometimes slightly thickened on the back, although much less so than those of *Q. lobata*, and sometimes are thin and not distinguishable from those of *Q. Douglasii*.

Miss *Alice Eastwood*, September 18, 19, and 20, 1894 (nos. 44, 154, 155, 156, 163, 164 type, 165).

Quercus Comptonae, n. hyb. (*Q. lyrata*×*virginiana*).—*Q. lyrata* Sargent (not Walter), Silva N.Am. **8**:48 in part. *pl. 374. figs. 5, 8.* 1895.—Leaves oblanceolate, acuminate at apex, gradually narrowed into a long cuneate entire base, deeply repandly lobed with 3 or 4 pairs of nearly triangular lateral lobes pointing forward; covered above with scattered fascicled hairs and coated below with soft close pubescence when they unfold, becoming thick, dark green, glabrous and very lustrous on the upper surface, pale and pubescent on the lower surface, 6–9 cm. long and 3–4 cm. wide, with slightly thickened revolute margins, prominent glabrous midribs, and veins extending to the points of the lobes; on the lower branches often broadly obovate, rounded or abruptly acute and slightly 3-lobed at apex, or rarely entire and sometimes 10 cm. long and 6 cm. wide; petioles pubescent early in the season, becoming glabrous, about 1 cm. in length. Staminate flowers in slender villose aments; calyx sparingly villose, divided to below the middle into 5 rounded lobes much shorter than the slender filaments; anthers short-oblong, apiculate, glabrous. Pistillate flowers hoary-tomentose, single or in pairs, or rarely in threes, on slender pubescent peduncles 2–4 cm. long. Fruit ripening at the end of the first season; nuts

oval to oblong-ovate, abruptly pointed, light chestnut brown, about 2.5 cm. long and 1.5–1.8 cm. in diameter, inclosed for two-thirds or three-quarters of their length in the thin deep cup-shaped cup, the scales all thin, broadly ovate, narrowed and abruptly short-pointed at apex, pale pubescent, their tips free, those of the upper ranks forming a serrate rim to the cup.

A tree sometimes 35 m. high, with a tall straight trunk 1–1.5 m. in diameter, covered with deeply furrowed dark red-brown bark, erect and spreading branches forming a broad head, and slender branchlets sparingly pubescent when they first appear, and glabrous, lustrous, and light reddish brown at the end of their first season. Winter buds ovate-oblong, acute, about 0.05 cm. in length, their scales light chestnut brown, puberulous.

Duncan Park, Natchez, Adams County, Mississippi, Miss *C. C. Compton* and *C. S. Sargent* (no. 1, type), April 17, 1915, Miss *Compton*, November 1915.

ALABAMA.—Near an abandoned house in sandy soil 30 miles west of Selma, Dallas County, *T. G. Harbison* (no. 10), April 20 and October 21, 1915.

LOUISIANA.—Audubon Park and streets of New Orleans, *R. S. Cocks*, October 1911.

TEXAS.—Banks of Peyton's Creek, Matagorda County, *C. Mohr*, December 18, 1880.

Specimens of this tree appear to have been first collected by Dr. MOHR in Texas. These specimens were referred by me in The Silva of North America to *Q. lyrata*, with the statement that these were the only acorns of *Q. lyrata* I had seen with cups inclosing only one-half or two-thirds of the nut. The Texas tree or trees have probably disappeared, as *E. J. Palmer* has failed to find them in a careful search along both banks of Peyton's Creek from source to mouth. I first saw this tree in Duncan Park, Natchez, on the estate of the late Dr. STEPHEN DUNCAN, where there is a large specimen in the rear and not far from the Duncan mansion. Later Miss COMPTON succeeded in locating 20 or 30 of these trees in Natchez and its neighborhood. They are all large trees in the neighborhood of dwellings with the exception of two seedlings growing in the woods near the city. The largest and handsomest of these trees which I have seen is growing in the garden of St. Joseph's School, on State Street, Natchez. Another very large tree is standing in "Magnolia Vale" under the bluff at Natchez. The trees in New Orleans which are not large are said to have been brought from across Lake Pontchartrain 30 or 40 years ago, but Professor COCKS, who has carefully searched for this oak, has failed to find any trees in Louisiana with the exception of those planted in New Orleans. The Texas trees seen by MOHR may have been growing naturally in the woods, but all the others now known, with the exception of the two or three young trees which have sprung up naturally in the woods near Natchez, are evidently trees that have been planted. I am inclined

to believe that this oak is a hybrid probably between *Q. lyrata* and *Q. virginiana*. The shape and texture of the leaves suggest the former, but they are thicker and more lustrous than those of *Q. lyrata*. In these characters and in their pubescence they resemble those of *Q. virginiana*. The long-stalked fruit with the thin cup-scales has a general resemblance to the fruit of the live oak; from that of *Q. lyrata* it differs in the scales of the cup which are never thick at the base, in the shape of the cup pubescent on the inner surface, that of *Q. lyrata* being glabrous, and in the shape of the oblong-ovate nuts, which are never subglobose or short-ovate like those of *Q. lyrata*. The hybrid origin of *Q. Comptonae* is further borne out by the fact that H. NESS has raised artificially a hybrid oak between *Q. lyrata* and *Q. virginiana*, the fruit and the leaves of which, although smaller than those of the Mississippi trees, almost exactly resemble them in shape.

I take much pleasure in naming this tree, which is one of the handsomest American oaks, for Miss C. C. COMPTON, of Natchez, who has worked industriously to make it possible for me to understand it, and who has greatly aided the Arboretum by gathering material of the woody plants of Adams County, Mississippi.

Quercus Harbisonii, n. hyb. (*Q. stellata* var. *Margaretta*×*virginiana* var. *geminata*).—Leaves oblong-obovate to oblong, rounded at apex, gradually narrowed and cuneate at base, 3- or 5-lobed with acute or rounded apiculate lobes, or nearly entire with irregularly undulate margins and occasionally furnished with one or with two minute lobes below the middle; at maturity thick, bluish green, scabrate and lustrous on the upper surface, covered on the lower surface with loose pubescence, 6–7 cm. long and 2–4.5 cm. wide, with thickened slightly revolute margins, pubescent midribs and veins, and conspicuous reticulate veinlets. Flowers and spring leaves not seen. Nut oblong-ovate, gradually narrowed and rounded at apex, light chestnut brown and lustrous, about 2 cm. long, inclosed for one-third of its length in the turbinate cup covered with closely appressed hoary-tomentose scales, those near the base of the cup slightly thickened on the back.

A tree 5–6 m. high, divided near the ground into two stems covered with rough gray bark, and slender reddish branchlets pubescent during their first season and dark reddish brown and nearly glabrous in their second year, and ovate obtuse winter buds covered with chestnut brown nearly glabrous scales.

A single tree in sandy soil, Jacksonville, Florida, *T. G. Harbison* and *C. S. Sargent*, December 3, 1917.

This plant has every appearance of being a *Q. stellata-virginiana* cross. The thickened leaves with thickened revolute margins and the conspicuous reticulate veinlets point to var. *geminata* of *Q. virginiana* as one of the parents; the narrow and often rounded lobes of many of the leaves, the character of the pubescence on their lower surface, and the slender reddish slightly pubescent branchlets and globose nearly glabrous buds point to var. *Margaretta* of *Q. stellata* as the other parent.

A small tree 4–5 cm. tall found by *E. J. Palmer* at Fort Chadbourn, Coke County, Texas, July 9, 1917 (no. 12463), is probably a hybrid between the typical *Q. virginiana* and one of the dwarf forms of *Q. stellata*, but without fruit it is not desirable to describe it.

In the hope of drawing attention to them, names are proposed for the following hybrid oaks, although the material available is not sufficient to make their description possible:

Quercus Lowellii, n. hyb. (*Q. borealis*×*ilicifolia*).

Seabury, York County, Maine, *Percival Lowell*, September 8, 1914 (without fruit).

Quercus oviedoensis, n. hyb. (*Q. cinerea*×*myrtifolia*).

Oviedo, Orange County, Florida, *T. G. Harbison*, May 29, 1917 (nos. 19, 20, type). A small tree with leaves intermediate in shape between those of its supposed parent.

Quercus Cocksii, n. hyb. (*Q. rhombica*×*velutina*).

Pineville, Rapides Parish, Louisiana, *R. S. Cocks*, April 18, 1917 (no. 4702, type). The leaves of this tree generally resemble in shape those of *Q. rhombica*, but occasionally are slightly lobed and are rusty and thickly covered below with pubescence.

Arnold Arboretum
Jamaica Plain, Mass.

UREDINALES OF THE ANDES, BASED ON COLLECTIONS BY DR. AND MRS. ROSE

J. C. Arthur[1]

The uredinalean flora of the highlands of western South America is a rich and varied one. This can be seen even from the scattered literature, for as yet no extended or monographic work covering this region has been published. Probably Chile has received the most attention, beginning with the 11 species included in Léveillé's paper of 1846 on "Descriptions des champignons de l'herbier du Muséum de Paris" (Ann. Sci. Nat. III. **5**:111–167, 249–304), and Montagne's treatment of the fungi in the eighth volume of Gay's "Historia fisica y politica de Chile," issued some 10 years later, down to the 21 species of rusts in Spegazzini's "Fungi Chilenses" of 1910. The article which includes the greatest number of rusts, however, and by far the most important single work treating of the Andean Uredinales, is Mayor's "Contribution à l'étude des Urédinées de Colombie" (Mém. Soc. Neuch. Sci. Nat. **5**:442–599), published in 1913. In this work are 158 species, of which 84 are described as new, and most of the species are admirably illustrated with drawings of the several forms of spores. Not all of these, however, are from the mountainous part of Colombia. A rough estimate will place the number of rusts now named from the Andes at about 250 species, which is probably not half the total number eventually to be found.

For more than three-quarters of a century explorers and travelers have picked up, more or less incidentally, the parasitic fungi of the Andes, and when the day comes for a comprehensive and inclusive study of all available material, the man who has patience and ingenuity to bring together this widely scattered wealth of material will find no mean resources for a systematic account of an interesting region. Probably specimens oftenest encountered in herbaria are

[1] Reprints may be obtained by application to the Botanical Department, Purdue University Agricultural Experiment Station, Lafayette, Ind., under whose auspices the work was carried on.

those collected by Dr. G. VON LAGERHEIM, the eminent mycologist of Stockholm, Sweden, who spent some time at Quito, Ecuador. He published no connected account of his work at Quito, although in a "vorläufige Mittheilung," describing 4 new genera (Ber. Deutsch. Bot. Gesell. **9**:344. 1891), he speaks of "my detailed 'Monographie der Uredineen Ecuadors,' now in course of completion." He, however, distributed his material freely, not only the specimens which he was able to positively identify, but others as well, partly unnamed and partly with suggested names for forms that appeared to be new species. This mine of rich material, for many strange forms are being uncovered from time to time and placed in newly erected genera or made to explain obscure relationships, has been drawn upon in the present paper, and 3 of the LAGERHEIM species are here published, one in a new genus, and all in genera other than previously suggested.

The present contribution to the rusts of the Andes, with the exception of 3 collections by LAGERHEIM and two by ULE, comprises material secured by Dr. and Mrs. J. N. ROSE during a South American exploration in 1914 primarily for cacti. Dr. ROSE's broad botanical interests and generous disposition toward workers in other botanical lines than his own were shown in his letter of May 8, 1914, to the writer, announcing his proposed trip: "You will probably be surprised," he says, writing from the National Museum, "to learn that Mrs. ROSE and I plan to leave here (Washington, D.C.) about June 10 for an extended trip through western South America, especially Peru and Chile. I wonder whether it will be worth while to collect any of the parasitic fungi." Upon assuring him that the region to be visited was one of more than ordinary interest to American uredinologists he wrote shortly before departing: "I shall take great pleasure in collecting all of this kind of material (rusts) that I can."

In transmitting the rust collections, 40 numbers in all, after his return from 6 months in South America, he says: "I fear that you will be disappointed that there are so few of them," and as explanation for the small number, "because I have been trying to collect parasitic fungi where none grew," in the dry regions of western South America where species of *Cactus* most abound. He also felt

that "most of them must be common things, as they were picked up on weeds."

Perusal of the following account will reveal the value of keeping rust collecting "in mind all summer," even in a region where rusts do not flourish. Twenty-two collections are of species that may be called widespread and common, most of them on what might be designated as weeds, two-thirds belonging to a single species of *Coleosporium*. Although these were well worth collecting to illustrate geographical and host distribution, yet the other 18 collections receive the chief attention, as they embrace 6 new species and 6 species not often found. Altogether the 40 numbers drop into 21 species of Uredinales, of which about one-fourth require to be described as new, as many more are rare and little known forms, while only about one-third can be called common. The results should be gratifying to Dr. and Mrs. ROSE, and certainly will be particularly helpful to students of the rust portion of the Andean flora. Four species by other collectors make a total of 25 species here recorded.

1. COLEOSPORIUM SENECIONIS (Pers.) Fries (on Carduaceae).—*Senecio adenotrichos* DC.,[2] Palos Quernados, Chile, October 4, II, no. 19188; vicinity of Choapa, Chile, October 6, II, no. 19194; vicinity of Illapel, Chile, October 6, II, no. 19238; Las Palmas, Chile, October 16, II, no. 19363; west of La Ligua, Chile, October 22, II, no. 19390.—*S. fistulosus* Poepp. (?), vicinity of Choapa, Chile, October 6, II, no. 19196.—*S. glabratus* H. and A., Los Molles, Chile, October 22, II, no. 19398.—*S. hakeaefolius* Bert., vicinity of Illapel, Chile, October 6, II, no. 19248; La Serena, Chile, October 9, II, no. 19267.—*S. thinophilus* Phil. (?), vicinity of La Serena, Chile, October 10, II, no. 19288.—*S. vulgaris* L., Santa Inez, Chile, October 16, II, no. 19497.—*Senecio* sp., Cerro Grande, Chile, October 10, II, no. 19495; vicinity of La Serena, October 11, II, no. 19312; La Paz, Bolivia, August 15, II, no. 18909.

It is remarkable that this rust, very common in Europe, should be so abundant in Chile, and apparently also in Argentina, while it is yet practically a stranger in North America. The aecia occur

[2] All collections are to be credited to Dr. and Mrs. J. N. ROSE, and for the year 1914, unless otherwise stated.

on the leaves of pine. It was collected at Providence, Rhode Island, in 1883, on *Senecio vulgaris*, but apparently soon disappeared, and has not been reported again from any station in North America.

It will be observed that all the collections recorded, most of them being very ample, contain no telia. This may indicate that the aecia on pine are rare or absent from the region, and that the rust is reproduced by means of its urediniospores chiefly or wholly.

2. CHRYSOCELIS LUPINI Lagerh. and Diet. (on Fabaceae).—*Lupinus paniculatus* Desr. (?), Cuzco, Peru, September 1, III, no. 19050.

The genus *Chrysocelis* was founded in 1913, upon studying material from Colombia, submitted by Dr. EUG. MAYOR to Dr. P. DIETEL (MAYOR, Contribution à l'étude des Urédinées de Colombie, Mém. Soc. Neuch. Sci. Nat. **5**:542–544). The type is on an undetermined species of *Lupinus* from near Bogota at 3000 m. altitude (no. 95), and accompanied by another collection from the same region at 2600 m. (no. 95a). These specimens were compared with similar collections made by LAGERHEIM in Ecuador 20 years earlier on 3 species of *Lupinus*, one of which has been examined by the writer.

This is a rust quite unlike any other known. It is a long cycle form with pycnia, aecia, and telia, and in all collections previously recorded sori of both aecia and telia are present. In the discussion following the founding of the genus, the somewhat unusual nature of the aecia, and the doubtful affinities of the rust are considered. From my own study I am inclined to dissent from the tentative conclusion that the rust is not to be referred to the Uredinaceae (Melampsoraceae), but to the Aecidiaceae (Pucciniaceae), because of the superficial character of the telia and the lack of lateral adhesion of the teliospores. Both of these conditions can be harmonized, I believe, with requirements for the former family, rather than the latter, and such characters as the cylindrical and sessile teliospores, and the highly pulverulent spore chains of the aecia, or possibly they are uredinia, would further lend countenance to this view.

3. **Uropyxis quitensis** Lagerh., sp. nov. (on Berberidaceae).—*Berberis* sp., Quito, Ecuador, April, 1891, II, III, *G. Lagerheim.*

Uredinia and telia hypophyllous, few, but with numerous spores scattered over the leaf surface, yellowish; urediniospores globoid or broadly ellipsoid, 19–23 by 23–24 μ, the wall nearly or quite colorless, finely and closely echinulate, thin, 1 μ, the pores indistinct; teliospores broadly ellipsoid, 20–23 by 21–26 μ, rounded at both ends, or flattened and sometimes introverted by drying, slightly or not constricted at septum, the wall pale cinnamon brown or nearly colorless, thin, 1–1.5 μ, smooth, the pores obscure but seemingly lateral; pedicel short, fragile, usually attached more or less obliquely, breaking away near the spore.

The spores are more delicate than in other known species of the genus, and the germ pores correspondingly more indistinct. It is also the first species to show smooth teliospores, although in *U. texana* they are so little roughened as to appear smooth by the usual method of examination. The obliquely attached pedicels and the thin walls of the teliospores evidently led LAGERHEIM to attach the tentative name of *Sphenospora quitensis* to the specimens which he distributed.

Cleptomyces, gen. nov.

Cycle of development includes pycnia and telia, both subepidermal.

Pycnia flask-shaped, with ostiolar filaments.

Telia erumpent, definite; teliospores pedicillate, 2-celled with transverse septum; wall laminate, inner layer firm, colored, outer layer more or less hygroscopic, colorless, overlaid by the verrucose cuticle, the pores 4 or more and equatorial or scattered.

Type species, *Puccinia Lagerheimiana* Dietel (Hedwigia **31**: 288. 1892).

4. **Cleptomyces Lagerheimianus** (Dietel), comb. nov. (on Verbenaceae).—*Aegiphila* sp., Toldo near Riobamba, Ecuador, August 1891, O, III, *G. Lagerheim.*

This short cycle species from the Ecuadorian province of Chimborazo was styled by DIETEL "a very remarkable one" in his extended comments following the original technical description of *Puccinia Lagerheimiana*. He was especially impressed with the number and arrangement of the germ pores, but decided that these did not constitute sufficient grounds on which to remove it from the

genus *Puccinia*. Ten years later, however (Hedwigia Beibl. **41**: 112), he placed it under *Uropyxis*, a genus which he considered well separated from *Puccinia* and *Phragmidium* by the following group of characters: (1) multiple number of germ pores, (2) formation of a hygroscopic layer in the wall, (3) inclination toward the production of more than two cells in the spore, these characters all applying to the teliospore.

It was an important advance in recognizing the need of a group of characters in delimiting genera among the rusts. Not until 1905, when the writer presented a classification of the rusts before the Vienna Congress, was the principle extended to include characters from all the stages in the life cycle, and foremost of all from the nature of the cycle itself. Unfortunately, such a criterion for rust genera is yet too little recognized.

The combination of characters used to establish the present genus is: (1) the short life cycle, (2) subepidermal pycnia, (3) more than two germ pores, (4) a hygroscopic layer, (5) a closely verrucose cuticle. Characters 1 and 4 ally the genus with *Calliospora*, the correlated short cycle form of *Uropyxis;* characters 3 and 5 with *Phragmidium;* but in no genus heretofore recognized is the full combination of characters to be found.

The germ pores in this species appear somewhat variable, but are usually 5 and approximately equatorial. The surface of the spores is moderately and closely verrucose, almost rugose-verrucose. The pedicel is fragile, and usually breaks away close to the spore. A rather full description of the species is given in SYDOW, Monog. Ured. **1**:843.

5. **Sphenosporea Berberidis** Lagerh., sp. nov. (on Berberidaceae).—*Berberis glaucescens* St. Hil. (?), Tahatanga, Ecuador, September 1891, III, *G. Lagerheim.*

Uredinia and telia hypophyllous, segregated on somewhat discolored spots; urediniospores globoid or broadly ellipsoid, 19–22 by 23–26 μ; wall pale cinnamon brown or colorless, 1.5–2 μ thick, moderately echinulate, the pores obscure; teliospores ellipsoid or elliptic, 21–24 by 26–32 μ; wall pale cinnamon brown, thin, 1 μ, slightly thicker above, 1.5–3 μ, smooth; pedicel colorless, as long as the spore, fragile, breaking off near the spore.

The species was distributed by LAGERHEIM with the herbarium name *Diorchidium Berberidis*. It appears, however, to be a genuine member of the genus *Sphenospora*, as judged by the exactly vertical septum, the thin and smooth walls of the teliospores, and other characters of both urediniospores and teliospores. The urediniospores were few in the specimen examined. The pores of the teliospores were not demonstrated, but seem to be apical. The pores in the genus *Diorchidium* are lateral, and only the type species on a Fabaceous host from south Africa is yet known, although *Puccinia Piptadeniae* P. Henn. from Brazil may prove to belong in the genus when well studied.

The host was given as *Berberis glaucophylla* on the packet, which was doubtless intended for *B. glaucescens*, although the determination has not been established. The leaves are large, thin, and markedly glaucous beneath.

6. UROMYCES LEPTODERMUS Sydow (on Poaceae).—*Panicum barbinode* Trin., Santa Clara, Peru, July 18, II, no. 18723.

A common and widely distributed species of warmer regions. It reaches northward through Central America and the West Indian Islands to central Mexico and southern Florida. It also occurs in India. The aecia are unknown.

7. UROMYCES CRASSIPES Diet. and Neg. (on Polygonaceae).—*Rumex cuneifolius* Campd., below Cuzco, Peru, September 2, II, no. 19070.

The species has been collected on the same host in the vicinity of Concepción, Chile, as stated by SPEGAZZINI in his "Fungi Chilenses" (p. 16). The species was also collected at Ollantaytambo, Peru, at 3000 m., apparently on the same host and showing uredinia only, May 17, 1915, *Cook* and *Gilbert* 783.

8. UROMYCES ELATUS Sydow (on Fabaceae).—*Lupinus saxatilis* Ulbrich (?), vicinity of La Paz, Bolivia, August 12, O, III, no. 18863.—*L. tomentosus* DC., below Pampa de Arrieros, Peru, August 23, I, no. 18962.

The species has rarely been collected. The aecia are conspicuous and have long peridia when fully developed. The telia are usually closely associated with the aecia; they are very small,

and give only a powdery appearance to the surface, the teliospores being small, thin-walled, very pale, and germinating freely upon maturity.

9. UROMYCES HOWEI Peck (on Asclepiadaceae).—*Asclepias curassavica* L., vicinity of Lima, Peru, July 24, II, no. 18770.

A very common species of rust throughout North and South America. Only uredinia are collected, except in the north temperate part of the range.

10. UROMYCES CESTRI Mont. (on Solanaceae).—*Cestrum* sp., Illapel, Chile, October 7, I, no. 19275.

The species was first described from the island of Juan Fernandez, Chile, in 1835, and is now known as a common tropical rust of both North and South America.

11. **Puccinia Bambusarum** (P. Henn.), comb. nov. (on Poaceae).—*Arundinaria* sp.

An ample portion of the type collection of *Uredo Olyrae* P. Henn. (Hedwigia **43**:164. 1904) recently became available for study. On this material there were found not only uredinia, but also telia. The latter are so small and inconspicuous as to easily escape notice. The collection, only one having been recorded so far under this name, was made in the northeastern part of Peru and in the plain region some distance from the high mountains, but for convenience the discovery of the teliospores may be recorded here.

Uredo Olyrae was reported to be on *Olyra* sp., a genus belonging to the tribe Paniceae, but upon examining the material now in the Arthur herbarium, Mrs. AGNES CHASE, agrostologist of the Department of Agriculture, Washington, says "there is no known species of *Olyra* with bristles at the summit of the sheath as in this specimen. These bristles are found in several genera of bamboos. I think this specimen is a species of *Arundinaria*." The specimen examined was distributed as "E. Ule, Appendix Mycothecae Brasiliensis, no. 5, Peru, Iquitos, 1902." A part of the same type collection, kindly sent to me in 1913 from the Berlin Museum, gives the collector's no. 3161 and the date July 1902.

In a similar way examination of type material of *Uredo Bambusarum* P. Henn. (Hedwigia **35**:255. 1896) discloses both uredinia

and telia, agreeing closely with the preceding. This collection was made in the state of St. Catharine, Brazil, and published as on *Bambusa* sp., *E. Ule* 866. A part of the same collection sent me by E. W. D. HOLWAY supplies the additional data "Blumenau, July 1888," and gives the host as "*Olyra micrantha*." Mrs. AGNES CHASE has examined this material and considers that it is some kind of bamboo, not identical with the preceding, and very probably *Arundinaria amplissima*, a species not uncommon in Brazil.

The two forms are herewith combined under one name. The following emended description is drawn from the original collections by E. ULE. From a misinterpretation of the specific characters the name *Uredo Olyrae* was introduced into the literature of the North American rusts (Mycologia **8**:21. 1916), but the error was corrected later (*ibid* **9**:92. 1917).

Uredinia amphigenous, scattered, elliptical, small, 0.5 mm. or less long, cinnamon brown; paraphyses none; urediniospores ellipsoid or obovoid, 18–23 by 23–29 μ; wall pale yellow or light golden brown, thin, 1–1.5 μ, rather sparsely and prominently echinulate, the pores obscure.

Telia few, like the uredinia in size and position, early naked, slightly darker in color; teliospores irregularly ellipsoid, often with the septum oblique, very small, 12–15 by 18–26 μ, rounded above, somewhat tapering below, slightly constricted at septum; wall cinnamon brown, moderately and uniformly thin, about 1.5 μ, smooth; pedicel colorless, one-third length of spore or less.

12. **Puccinia Roseanae,** sp. nov. (on Amaryllidaceae).—*Tecophilaea Roseana* Esposto ined., vicinity of Santa Clara, Peru, July 6, I, III, no. 18608.

Pycnia chiefly epiphyllous, numerous in loose groups, honey yellow becoming light brown, conspicuous, subepidermal, flask-shaped, about 130 μ in diameter.

Aecia hypophyllous, crowded in annular groups 3–6 mm. across, on larger discolored spots, cupulate, 0.2–0.4 mm. in diameter, the margin somewhat reverted, erose or lacerate; peridial cells rhomboidal, 18–26 by 22–30 μ in face view, abutted or slightly overlapped, the inner surface verrucose; aeciospores globoid, 16–23 by 18–27 μ; wall nearly or quite colorless, thin, 1 μ, inconspicuously verrucose.

Telia epiphyllous, scattered, oblong, 0.5–0.8 mm. long, prominent, long covered by the gray epidermis, light chestnut brown,

somewhat pulverulent, ruptured epidermis conspicuous; teliospores oblong, 23–27 by 42–52 μ, rounded at both ends, slightly or not constricted at septum; wall cinnamon brown, 2.5–3 μ thick, thicker above by addition of a pale umbo, 5–7 μ, with prominent, longitudinal ridges 3–5 μ apart; pedicel colorless, as long as the spore, fragile.

It is a pleasure to have the privilege of dedicating this striking new species of rust to Dr. and Mrs. J. N. ROSE, whose interest in the broad aspects of systematic botany could no better be attested than by the interesting collection of rusts reported in this article, made while studying the habits and distribution of certain groups of flowering plants. The rust is apparently quite unlike any previously described species, and occurs on a rare host, dedicated to Dr. ROSE.

13. **Puccinia Mogiphanis** (Juel), comb. nov. (on Amaranthaceae).—*Achyranthes* sp., Oroya, Peru, July 14, III, no. 19498; Pasco, Peru, August 6, II, III, no. 18804.

The material submitted by Dr. and Mrs. ROSE agrees in its uredinia with type material (Vestergren, Micr. Rar. Sel. 794) of *Uredo Mogiphanis* Juel (Bih. K. Sv. Vet.-Akad. Handl. **23**(3)^{10}:24. *fig. 35.* 1897), but shows in addition an abundance of telia. JUEL describes and figures the urediniospores as thin-walled, probably due to mistaking the cuticle for the whole wall, and the thick inner portion of it for cell contents. The wall is in fact 3–4 μ thick, and when well matured somewhat darker than indicated by JUEL. The pores are often 3 or 4, and somewhat equatorial, although more often 6 and unmistakably scattered, as JUEL says.

The telia are amphigenous, 0.5–1 mm. across, similar to the uredinia, soon naked, chestnut brown. The teliospores are ellipsoid or obovoid, 29–31 by 39–50 μ, rounded at both ends, or somewhat narrowed at base, slightly constricted at septum. The wall is chestnut brown, 2.5–3.5 μ thick, becoming noticeably thicker above, 7–10 μ. The pedicel is one to one and a half times the length of the spore, 7–9 μ thick and hyaline.

It is to be regretted that the Amaranthaceous hosts of neither the type material of *Uredo Mogiphanis*, collected in Brazil in 1904, and said to be on *Mogiphanes*, nor of the present collections from

Peru, have been specifically determined. ENGLER and PRANTL in their *Pflanzenfamilien* include *Mogiphanes* and *Telanthera* under *Alternanthera*, and all three appear to be the same as *Achyranthes*.

14. PUCCINIA MALVACEARUM Mont. (on Malvaceae).—*Malva sylvestris* L., Palos Quernados, Chile, October 4, no. 19186; Las Cardas, Chile, October 14, no. 19344.—*Malvastrum capitatum* (Cav.) Griseb., Copiapó, Chile, October 12, no. 19322.

A short cycle species and one of the commonest and best known rusts, which has spread from its original center in the Andes to all parts of the world where members of the Malvaceae grow.

15. PUCCINIA HYDROCOTYLES (Link) Cooke (on Ammiaceae).—*Hydrocotyle bonariensis* Lem., vicinity of Lima, Peru, July 24, II, no. 18768.—*H. ranunculoides* L.f., vicinity of Choapa, Chile, October 6, II, no. 19192.

A long cycle rust, usually gathered in the uredinial stage. The initial stage is not definitely known. It is not uncommon throughout South America, as well as northward into the United States.

16. **Puccinia Nicotianae,** sp. nov. (on Solanaceae).—*Nicotiana tomentosa* Ruiz and Pav., Santa Clara, Peru, July 18, O, I, III, no. 18722.

Pycnia epiphyllous, small, inconspicuous, honey yellow becoming darker, subepidermal, globose or flask-shaped, 112–120 μ wide.

Aecia epiphyllous, scattered, low cupulate, 0.1–0.2 mm. in diameter; peridium colorless, the margin recurved and lacerate; peridial cells loosely joined, abutted; aeciospores ellipsoid or globoid, 13–18 by 16–19 μ; wall pale yellow or colorless, thin, 1–1.5 μ, finely and inconspicuously verrucose.

Telia epiphyllous, scattered, among and in the old aecial cups, round, small, 0.1–0.2 mm. across, early naked, somewhat pulverulent, blackish brown, ruptured epidermis evident; teliospores ellipsoid or obovoid, 19–24 by 31–40 μ, usually rounded at both ends, sometimes narrowed below, not or only slightly constricted at septum; wall dark chestnut brown, 2.5–3 μ thick, somewhat thicker above up to 5 μ, finely and sparsely verrucose; pedicel tinted, short, fragile.

17. **Puccinia Acnisti,** sp. nov. (on Solanaceae).—*Acnistus arborescens* Schl., Santa Clara, Peru, July 18, O, I, III, no. 18722a.

Pycnia epiphyllous, appearing scattered or somewhat grouped, honey yellow becoming dark brown, noticeable, subepidermal, globoid, 70–125 μ in diameter.

Aecia amphigenous, appearing scattered or somewhat grouped, short cylindric, 0.1–0.2 mm. in diameter, 0.3–0.7 mm. high; peridium white, lacerate, soon falling apart; peridial cells rectangular or rhomboidal, 10–14 by 22–26 μ, slightly overlapping, the outer wall 3–4 μ thick, transversely striate, the inner wall about 3 μ thick, closely and somewhat coarsely rugose-verrucose; aeciospores ellipsoid, 16–19 by 19–27 μ; wall colorless or slightly tinted, 1–2 μ thick, finely and closely verrucose.

Telia mostly epiphyllous, scattered, round, minute, 0.1–0.2 mm. in diameter, somewhat pulverulent, shining blackish brown, ruptured epidermis evident; teliospores ellipsoid or oblong, 19–24 by 27–35 μ, rounded at both ends, slightly or not constricted at septum; wall dark chestnut brown, uniformly 2.5–3 μ thick, smooth; pedicel yellowish, slightly darker above, somewhat fragile.

18. Puccinia Spegazzinii DeToni (on Carduaceae).—*Mikania scandens* (L.) Willd. (?), Santa Clara, Peru, July 18, no. 18724.

A very abundant, short cycle rust, found throughout tropical America.

19. **Puccinia cuzcoensis,** sp. nov. (on Carduaceae).—*Baccharis floribunda* H.B.K. (?), Cuzco, Peru, September 1, I, II, no. 19054.

Aecia amphigenous, few, crowded in circinating groups, 3–5 mm. across, rather large, 0.2–0.4 mm. across, or confluent into curved sori 2 mm. long; peridium none, the epidermis overarched and rupturing centrally; aeciospores angularly ellipsoid or globoid, 21–26 by 29–35 μ; wall pale yellow or colorless, 2–3 μ thick, closely and finely verrucose.

Uredinia chiefly hypophyllous, numerous, scattered, roundish, 0.2–0.5 mm. across, early naked, pulverulent, chestnut brown, ruptured epidermis prominent; urediniospores rhombic-ellipsoid, 27–34 by 39–42 μ; wall golden or cinnamon brown, thick, 2.5–3 μ, very closely and rather bluntly echinulate, the pores large and distinct, 2, equatorial.

Telia not seen.

The species in its aecia, both from their caeomate structure and spores, is very much like *Puccinia Montoyae* Mayor, described on the same host from Bogota, but no teliospores are available with which to make a comparison, and the abundance of very conspicuous

uredinia is much in contrast to their entire absence in the Bogota material. The habitats are similar, but Bogota is a thousand miles or more north of Cuzco.

20. **Puccinia unicolor,** sp. nov. (on Carduaceae).—*Baccharis hemiprionoides* Bak., Cuzco, Peru, September 1, II, III, no. 19030.

Urediniospores intermixed with the teliospores, globoid or broadly ellipsoid, 21–23 by 23–26 μ; wall pale yellow, thin, 1–1.5 μ, closely and rather finely echinulate, the pores indistinct.

Telia hypophyllous, scattered, round, 0.2–0.5 mm. across, early naked, pulvinate, chestnut brown, ruptured epidermis inconspicuous; teliospores ellipsoid or oblong, 24–34 by 42–48 μ, rounded or obtuse at both ends, slightly constricted at septum; wall lemon yellow, thick, 2.5–3 μ, thicker above with slight trace of an umbo, 7–9 μ, smooth; pedicel somewhat tinted next the spore, as long as the spore, the wall thin, 1 μ.

The telia often thickly cover the under side of the whole leaf. The species is much like that of *P. sphenica* Arth., on *Baccharis sordescens* DC., from Mexico, but does not agree exactly, and the hosts are quite unlike.

21. Puccinia Spilanthis P. Henn. (on Carduaceae).—*Spilanthes ciliata* H.B.K., Santa Clara, Peru, July 18, II, III, no. 18727.

The species has been reported from Brazil and Argentina. It differs from *P. spilanthicola* Mayor, occurring on the same and other species of *Spilanthes* in Colombia, by the larger and paler teliospores, and the absence of mesospores. Although the teliospores germinate at maturity, yet in the present collection there occur intermixed urediniospores, not mentioned in the original description. They are globoid or obovoid, 24–29 by 26–34 μ, with a cinnamon brown wall, 1.5–2 μ thick, closely echinulate, and with 4 equatorial pores.

22. Puccinia sp. (on Carduaceae).

Genus and species undetermined, near Mollendo, Peru, August 25, II, III, no. 18986; same, O, I, II, III, no. 18987.

This is a species with smooth, ellipsoid teliospores and globoid, 2-pored urediniospores, belonging to the subfamily of hosts, Heliantheae, but cannot be exactly located.

23. **Aecidium Enceliae,** sp. nov. (on Carduaceae).—*Encelia canescens* Cav., vicinity of Arequipa, Peru, August 3, no. 18792.

Aecia hypophyllous, scattered over the whole leaf surface, cylindric, large, 0.5–0.8 mm. in diameter, 0.5–1 mm. high, at first incurved, then erect, the margin erose; aeciospores globoid, 18–21 by 21–26 μ; wall colorless, thin, 1–1.5 μ, appearing smooth.

No aecia have been reported before on this host. There is a *Puccinia Enceliae* Diet. and Holw. known from Mexico, but no aecia have been associated with it as yet, and the chances that the present collection should be referred to it are few..

24. UREDO sp. (on Carduaceae).—*Baccharis* sp., vicinity of La Paz, Bolivia, August 9, no. 18840.

This collection, showing only uredinia, and with the host specifically undetermined, cannot be located with any degree of confidence.

25. UREDO ERYTHROXYLONIS Graz. (on Erythroxylonaceae).—*Erythroxylon Coca* Lam., La Paz, Bolivia, August 16, no. 18916.

A common rust wherever coca is cultivated. No other stage in the life cycle is known. In the present collection fully 50 per cent of the spores are distinctly paler in their lower part than above.

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AECIAL STAGE OF PUCCINIA OXALIDIS

W. H. Long and R. M. Harsch

In July 1915 the junior writer collected an undescribed *Aecidium* on the leaves of *Berberis repens* in Bear Canyon, located in the Sandia Mountains about 15 miles east of Albuquerque, New Mexico. At the time the *Aecidium* was discovered no clue was found as to what hosts might harbor the alternate stages of this rust. The marked differences in the microscopic characters of the new *Aecidium* easily separated it from the aecial stage of both *Puccinia graminis* and *P. koeleriae*, the only two other rusts known to occur on species of *Berberis*. The first assumption was that this new rust might have its alternate stage on some graminaceous host, but careful field work in the spring of 1916 by the senior author soon dispelled this theory, since this *Aecidium* was often found abundantly in localities where there were no possible grass hosts. Field observations showed that this rust always occurred in localities where plants of *Oxalis violacea* and *Berberis repens* were closely associated, and when they were not associated no rust was found on the *Berberis*. Later in the spring of 1916 the senior writer found young leaves of *Oxalis violacea* bearing the primary urediniospores of *Puccinia oxalidis* in direct contact with the old aecia which had sporulated. This association of the two rusts was constant throughout the canyons in the Sandia Mountains, where the two hosts occurred in proximity to each other, while neither rust was found on either host when the hosts were widely separated.

With this positive field clue as a guide, inoculations were made at Tejano Experiment Station, in the Sandia Mountains, about 30 miles from Albuquerque, on 10 wild plants of *Berberis repens* growing in the open. After thoroughly wetting the plants, living old leaves of *Oxalis* bearing germinating teliospores of *Puccinia oxalidis* were placed above young leaves of *Berberis*. Both inoculated and check plants were protected by placing tin cans over them. These inoculations were made September 20, 1916. The tin cans were removed September 23. On October 20 the 10 inoculated

plants were examined and all of them were found to be infected; some so badly that the leaves were dying, while all (6) of the check plants were healthy. At this date pycnia only were present, exuding droplets of a sweetish sticky fluid like honey-dew. Another trip was made to the Station June 30, 1917, when the inoculated leaves showed well developed aecia, while the check plants were still free of the rust. These inoculations were not considered absolutely conclusive, however, since the *Berberis* plants inoculated were in the open and therefore subject to external contamination.

In the fall of 1916 bulbs of *Oxalis violacea* were transferred from the mountains to Albuquerque, a distance of some 15 miles from any *Berberis* plants, and therefore free from any possible external contamination. Fresh but non-sporulating material of the *Aecidium* on *Berberis* was obtained from Bear Canyon June 22, 1917. At this time no *Oxalis* plants had appeared above ground in the vicinity of the infected *Berberis* leaves in the Canyon, but the *Oxalis* plants transferred to Albuquerque the preceding fall were in full leaf. The infected *Berberis* leaves were moistened and kept overnight under a bell jar to start sporulation. On June 23 two species of *Oxalis* (*O. violacea* and *O. stricta*) were inoculated under control conditions with the aeciospores from *Berberis*. Bell jars were kept over the plants 60 hours. Checks were also made. On June 30 many of the inoculated leaves of *O. violacea* had the typical uredinia of *Puccinia oxalidis*, while the check plants as well as all plants of *O. stricta* were free of the rust. July 22 telia were present on the inoculated leaves of *O. violacea*. The inoculations here reported, together with those made at the Tejano Experiment Station, prove conclusively that the new *Aecidium* on *Berberis repens* is the alternate stage of *Puccinia oxalidis*, a description of which is herewith given.

Puccinia Oxalidis (Lev.) Diet. and Peck

O. Pycnia amphigenous but mainly epiphyllous, seated on pallid to slightly reddish spots 4–8 mm. in diameter, conspicuous, conic-globoid, honey-yellow becoming blackish brown, appearing in the fall of the year when the pycnospores are discharged in a

sweetish sticky liquid. In the spring when the aecia appear the pycnia are blackish brown.

I. Aecia hypophyllous, seated on pallid to reddish brown spots which later become dark brown, crowded in irregular annular groups 4–8 mm. across, aecia orange color when fresh, cylindrical, 1–1.25 mm. high by 0.15 to 0.2 mm. in diameter, peridium opening at apex very irregularly, very slow to open and very tough, segments slightly if at all reflexed, usually falling away piecemeal, peridial cells not overlapping, in face view irregularly oblong to polygonal, 10–17×17–27 μ, in side view pulvinate 14–17×20–24 μ, inner wall verruculose 2–2.5 μ thick, outer wall irregularly striate, 3–4 μ thick, walls colorless, content of cells orange; aeciospores irregularly oval, ovate to subglobose, angular, 10–13×13–17 μ, average for ten, 11×14.4 μ; walls colorless, faintly verruculose to smooth, 1.5–2 μ thick, pores indistinct.

On Berberidaceae: *Berberis repens* from New Mexico as follows: Bear Canyon by *R. M. Harsch*, July 7, 1915 (no. 5554);[1] by *Bartholomew* and *Long*, June 22, 1917 (no. 6281), material used for inoculating *Oxalis violacea* plants; by *Long*, August 2, 1917 (no. 6284); Tejano Experiment Station, by *Long* and *Seay*, June and July 1916 (nos. 6005, 6006, 6021, 6097); by *Long*, July 1917 (no. 6285), material obtained by inoculating *Berberis* plants September 20, 1916, with teliospores of *Puccinia oxalidis* from *Oxalis violacea* July 1917 (no. 6286).

II. Uredinia hypophyllous, subepidermal, in irregular to orbicular groups 2–6 mm. across, often confluent and covering entire surface of leaf, round, 0.1–0.3 mm. across, soon naked, at first orange buff and waxy, later fading somewhat and becoming pulverulent, ruptured epidermis inconspicuous; urediniospores globoid or elliptical globoid, 15–20×17–25 μ; walls thin, about 1 μ, minutely echinulate, germ pores uncertain.

III. Telia hypophyllous, in orbicular to irregular groups 2–5 mm. across, often confluent over entire leaf surface, subepidermal, ruptured epidermis inconspicuous, soon naked, orange buff, waxy, round, 0.1–0.3 mm. across. Teliospore ellipsoid to oval, 12–22×17–28 μ, rounded or obtuse at both ends, slightly or not at all constricted at septum; septum often oblique; walls colorless,

[1] All herbarium numbers cited in this article refer to the herbarium numbers of the senior writer.

smooth, thin, less than 1 μ thick; pedicel colorless, thick, about as long as spore.

On Oxalidaceae: *Oxalis violacea* from New Mexico as follows: Albuquerque, by *Long*, July 1917 (no. 6282), material obtained by inoculating with aeciospores from *Berberis repens* June 20, 1917; Tejano Experiment Station, by *Long* and *Seay*, July and September 1916 (nos. 6014, 6100, 6102). Also reported on following hosts: from Jamaica, *Oxalis martiana;* from Mexico, *Oxalis divaricata*, *O. latifolia*, *O. tetraneuris*, *O. trinervis*, *O. vallicola*, *Oxalis* sp.; from Texas, *O. violacea;* from Brazil, *O. neuwiedii*.

The roestelia-like aecia and other characters of this rust indicate its relationship in a general way to the genus *Gymnosporangium*, while some of its characters show affinity for the genus *Eriosporangium*, from which, however, its very tough, persistent peridium would exclude it. It does not belong to the genus *Argomyces*, where ARTHUR has provisionally placed it. If one were following ARTHUR'S nomenclature, the rust would probably belong to a new genus, but the writers prefer to leave it under the old genus *Puccinia* for the present.

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CURRENT LITERATURE

BOOK REVIEWS

New Jersey pine barrens

The coastal plain of New Jersey has long been famous for its unique vegetation. It probably shows the nearest approach to primeval forest in close proximity to a great center of population to be found anywhere. As a center of distribution of one group of species, and the area where two other groups, the one from the south and the other from the north, reach the limits of their range, it is equally noteworthy. These features, among others, have made its flora the subject of many papers, but in the present volume HARSHBERGER[1] has brought together within the pages of a single volume a vast collection of facts, both new and old, that will go far toward making its vegetation the most carefully studied and the best known upon the continent.

The treatment of the vegetation is essentially ecological in the broadest sense, some phases of plant study being included that do not often come within that category. As examples we may cite the descriptions of cranberry culture, of the collecting of drug plants, and of the turpentine industry. It is, however, principally in the analysis of the various plant communities that the ecological value of the work lies. Nine great natural divisions of the vegetation are recognized, of which the flat pine barren, with its forest of *Pinus rigida*, supplemented by a few *P. echinata* and several species of dwarf oaks, is the most unique and interesting. Aside from the pines and oaks, various Ericaceae are conspicuous, comprising species of *Vaccinium*, *Gaylussacia*, and *Kalmia*.

Pinus rigida receives careful study, not only in its place as the dominant tree in the characteristic association, but also in its individual development, its various growth forms being illustrated in not less than 37 well drawn sketches. In general, it is a small tree, little over 30 feet in height, but in addition to the tree forms various gradations to bush shapes and elfin-wood are distinguished.

In addition to the studies of the various plant associations, analysis of the vegetation according to JACCARD'S statistical method and RAUNKIAER'S life forms are presented. The biological spectrum shows the flora of the pine barrens to be particularly rich in hemicryptophytes and helophytes. In another chapter the phytophenology of the vegetation is presented, the time of flowering and fruiting being given for not less than 548 species. Not less

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[1] HARSHBERGER, JOHN W., The vegetation of the New Jersey pine barrens: An ecological investigation. 8vo. pp. xi+329. *figs. 284* and *map*. Philadelphia: Christopher Sower Co. 1916. $5.00.

interesting are detailed stem and root studies of individual species illustrated by 50 drawings, while the further ecological anatomy of the pine barren plants is considered in two chapters devoted respectively to leaf forms and leaf structure. The latter is illustrated by over 50 drawings of cross-sections studied microscopically.

These notes all go to show that the volume is full of innumerable data regarding the plant life of the region under consideration, making it one of the most comprehensive and complete ecological studies yet undertaken. These details are well organized and splendidly illustrated by numerous drawings, photographs, and maps. It forms an invaluable record of a more than usually interesting region, while the publishers have cooperated with the author in presenting it in an attractive volume.—GEO. D. FULLER.

Algae

WEST'S *British freshwater algae*, which was published in 1904, supplied a long felt want. Its convenient taxonomic keys, together with notes on habitats, life histories, and biological conditions, all written with the authority which comes only from first hand knowledge of the subject, made the book so indispensable that the edition was soon exhausted. After delays, occasioned partly by the author's illness and partly by the great war, the first volume[2] of a more extensive work has made its appearance. This volume is also the first of a still more extensive series which will appear under the general title of *Cambridge Botanical Handbooks*, now being edited by Professors SEWARD and TANSLEY. A volume on lichens by Miss LORRAIN SMITH, one on fungi by Dr. HELEN GWYNNE-VAUGHAN, and one on Gnetales by the late Professor PEARSON, are in an advanced stage of preparation.

The present volume on algae deals with the Myxophyceae (Cyanophyceae), Peridineae, Bacillariaceae, and Chlorophyceae, both fresh water and marine. No keys are given, a taxonomic account, excluding the diatoms and desmids, being reserved for the second volume. The treatment, however, follows the taxonomic sequence, the orders and sub-orders, families and sub-families appearing in succession, usually beginning with a diagnosis, followed by descriptions of habitats, biological conditions, structures, and life histories, and ending with a discussion of affinities. Each of the larger divisions closes with a list of the literature cited.

We are glad to see the Cyanophyceae included as the lowest of the algae. It will be remembered that OLTMANNS excluded this group from his book on the morphology and biology of algae. WEST does not agree with HEGNER, OLIVE, GARDNER, KOHL, PHILLIPS, and others who regard the central body as a nucleus. To us his arguments against the nuclear theory do not seem convincing, especially since the Cyanophyceae are so low in the scale of living organisms.

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[2] WEST, G. S., Algae. Vol. I. 8vo. pp. viii+475. *figs. 271*. Cambridge University Press. 1916. 25*s*.

In forms so simple in other respects, we might anticipate some simplicity in the nucleus. In making phylogenetic charts, there is even greater room for difference of opinion, but that room will become more and more restricted as the number of critical investigations increases. In regard to distribution, habitats, structure, and biology there is less room for dispute, and these subjects constitute the most interesting and valuable part of the book. The 271 illustrations, comprising 1284 lettered or numbered figures, are well drawn, and more than half of them are from the pen of the author.

The second volume, with its taxomonic keys, will be awaited with interest, for the cosmopolitan habit of most algae makes such keys almost as serviceable in the United States as in England.—CHARLES J. CHAMBERLAIN.

MINOR NOTICES

Ornamental trees of Hawaii.—A book[3] upon the introduced trees grown for ornamental purposes in the Hawaiian Islands, containing adequate descriptions and excellent illustrations, should prove a useful and a welcome source of inspiration and instruction to the residents of Honolulu and other similarly situated towns. To those living in other lands it shows the possibilities of tropical islands for the growth of many beautiful and remarkable trees and shrubs imported from other tropical countries. Among these trees the palms and the legumes stand preeminently first in importance, each family having devoted to its presentation a score or more of plates, while nearly double that number of species are described. The other families represented are too numerous to permit of enumeration. The descriptions are non-technical but apparently quite accurate. There is no attempt at any key to genera or species, although the importance of such an aid to identification is obvious. It is to be feared that without some such assistance and in spite of the numerous good illustrations the amateur botanists of Hawaii will encounter considerable difficulty in using the volume to further their acquaintance with introduced trees.—GEO. D. FULLER.

NOTES FOR STUDENTS

Taxonomic notes.—ARTHUR[4] has described a new genus (*Frommea*) of rusts, the type being *Uredo obtusa* Strauss on *Tormentilla erecta*.

BLAKE[5] has described two new species of *Polygonum*, *P. achoreum* occurring from Quebec and Vermont to Minnesota, Missouri, Montana, and Saskatchewan; and *P. allocarpum* occurring along the sea coast of Maine and adjacent islands of New Brunswick.

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[3] ROCK, JOSEPH F., The ornamental trees of Hawaii. 8vo. pp. v+210. *pls. 80.* 1917. Honolulu. H.I. Published under patronage.

[4] ARTHUR, J. C., Relationship of the genus *Kuehneola*. Bull. Torr. Bot. Club **44**:501–511. 1917.

[5] BLAKE, S. F., Two new Polygonums from New England. Rhodora **19**:232–235. 1917.

BURT[6] has monographed the genus *Merulius* in North America, recognizing 40 species, 16 of which are described as new. In connection with the description of each species, a full list of specimens examined is given.

DEARNESS[7] has described 38 new North American species of Ascomycetes, representing 28 genera.

EVANS[8] has described a new species of *Lejeunea* (*L. minutiloba*) occurring in Bermuda, Cuba, Porto Rico, and St. Thomas.

FERNALD[9] has described a new willow (*Salix Peasei*) from the White Mountains of New Hampshire. It is a "depressed shrub" trailing on wet mossy banks at an altitude of 4300–4500 feet.

GIBBS[10] in connection with a study of the Arfak Mountain region of New Guinea has included the descriptions of 90 new species by various authors. Among them are the following new genera: *Gibbsia* (Urticaceae), *Idenburgia* (Trimeniaceae), *Poikilogyne* (Melastomaceae), and *Palmervandenbroekia* (Araliceae). The new species are distributed as follows: Pteridophytes 7, Gymnosperms 2, Monocotyledons 26, Dicotyledons 55.

MAIRE[11] has published descriptions of new or little known fungi of northern Africa. The contribution includes 41 new species, distributed as follows: Phycomycetes 2, Ascomycetes 12, Ustilaginales 6, Uredinales 4, Autobasidiomycetes 4, Fungi Imperfecti 13.

MERRILL[12] has published a second paper on the flora of Borneo, describing 39 new species, and crediting about 25 additional ones to Borneo for the first time. The previous paper contained 48 new species and a new genus.

ROCK[13] has published a detailed account of the genus *Metrosideros* as represented in Hawaii. He recognizes 4 species, the most remarkable being the polymorphous *M. collina*. In fact, the name is *M. collina* subsp. *polymorpha*, under which 8 varieties are described, and 3 forms of as many varieties. The species, therefore, is treated as a trinomial, the varieties bearing 4 names and

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[6] BURT, EDWARD ANGUS, *Merulius* in North America. Ann. Mo. Bot. Gard. **4**:305–362. *pls. 20–22.* 1917.

[7] DEARNESS, JOHN, New or noteworthy North American Fungi. Mycologia **9**:345–364. 1917.

[8] EVANS, ALEXANDER W., A new *Lejeunea* from Bermuda and the West Indies. Bull. Torr. Bot. Club **44**:525–528. *pl. 24.* 1917.

[9] FERNALD, M. L., A new alpine willow. Rhodora **19**:221–223. 1917.

[10] GIBBS, L. S., A contribution to the phytogeography and flora of the Arfak Mountain, etc. London: Taylor and Francis. 1917. 12/6.

[11] MAIRE, R., Champignons Nord-Africains nouveaus on peu connus. Bull. Soc. Hist. Nat. de'l Afrique du Nord **8**:134–200. 1917.

[12] MERRILL, E. D., Contributions to our knowledge of the flora of Borneo. Jour. Straits Branch R. A. Soc. no. 76. pp. 75–117. 1917.

[13] ROCK, JOSEPH F., The Ohia Lehua trees of Hawaii. Bot. Bull. 4, Board of Agric. and For. Hawaii. pp. 76. *pls. 31.* 1917.

the forms 5 names. The numerous plates are reproductions of fine photographs.

SMALL[14] has described a new species of *Anamomis* (*A. Simsonii*) from the Everglades of Florida. The only other species of the genus known to grow in the United States is the endemic *A. dicrana*, which occurs in a different part of Florida.

SMITH,[15] in continuation of his studies of Malayan orchids, has described 66 new species, representing 24 genera. *Basigyne* is described as a new genus.

STURGIS[16] has described new species of Myxomycetes, chiefly from Colorado, in *Physarum* (2), *Didymium*, and *Enteridium*.

SMITH,[17] in continuation of his studies of *Lupinus*, has monographed the Microcarpi, recognizing 6 species, although 14 specific names have been published. The discussion of *L. densiflorus* with its varieties is reserved for a later paper. The variable species of the 5 considered is *L. subvexus*, 8 new varieties being described.

WERNHAM,[18] in continuation of his studies of tropical American Rubiaceae, has described a new genus (*Raritebe*) from Colombia, resembling *Bertiera*, the new name being an anagram of the latter. New species are also described in *Psychotria* (2) and *Palicourea* (4).—J. M. C.

Evaporation and soil moisture studies.—The increasing amount of attention given to quantitative studies of the moisture factors of various plant communities is shown by several recent papers. Conspicuous among them is one by WEAVER,[19] reviewed elsewhere in this journal, in which he reports measurements of the evaporating power of the air and of soil moisture in both forest and grassland associations of southeastern Washington, leading to the conclusion that "evaporation rates and the amount of soil moisture in the various communities vary in general directly with the order of their occurrence in the succession, the climax community being the most mesophytic in both respects." With regard to the former factor it is further stated that "a study of the differences of the rate of evaporation in the various plant communities shows that

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[14] SMALL, J. K., The genus *Anamomis* in Florida. Torreya **17**:221–224. *fig. 1.* 1917.

[15] SMITH, J. J., Orchidaceae novae Malayensis. VIII. Bull. Jard. Bot. Buitenzorg II. no. 25. pp. 103. 1917.

[16] STURGIS, W. C., Notes on new or rare Myxomycetes. Mycologia **9**:323–332. *pls. 14, 15.* 1917.

[17] SMITH, CHARLES PIPER, Studies in the genus *Lupinus*. II. The Microcarpi, exclusive of *Lupinus densiflorus*. Bull. Torr. Bot. Club **45**:1–22. *figs. 16.* 1918.

[18] WERNHAM, H. F., Tropical American Rubiaceae. X. Jour. Botany **55**:336–341. 1917.

[19] WEAVER, J. E., A study of the vegetation of southeastern Washington and adjacent Idaho. Univ. Neb. Studies **17**:no. 1. pp. 114. *figs. 48.* 1917.

these differences are sufficient to be important factors in causing succession, at least through the earlier stages, where light does not play an important rôle." These conclusions are supported by adequate data obtained in a region exhibiting a wide range of conditions, with successions comprising a considerable number of stages, and agree closely with the conclusions of the reviewer drawn from data obtained in northern Indiana.[20] These conclusions meet with the approval of CLEMENTS,[21] who admits evaporation to be a cause of succession since it affects the available moisture supply of the habitats.

Another investigation of the same moisture factors by WEAVER and THEIL,[22] while primarily concerned with contrasting the evaporating rates and soil moisture conditions of forest and grassland and demonstrating the greater xerophytism of the latter in both Minnesota and Nebraska, agrees perfectly in its conclusions regarding the relationship of these factors to succession with those of WEAVER already cited. It would also appear from the data contained in this report that the rather high evaporating power of the air in these grassland communities, together with the frequent lack of growth water during the growing season, may in a large measure account for the absence of trees in these regions except along the streams or in other more humid situations. The investigation thus forms a contribution to our scanty knowledge of the factors involved in causing the development of prairies.

GATES,[23] measuring the evaporating power of the air in various plant associations in Michigan, has obtained data that are quite similar to those of the investigators cited, but he reaches an almost directly opposite conclusion that the different rates of evaporation are the result and not the cause of succession. This disagreement with the conclusions of WEAVER and with those of the reviewer, both supported by larger quantities of data, seems to be due not so much to a confusion of cause and effect as to the facts that (1) GATES'S investigation was conducted in a region much more humid than those studied by the other workers, as shown by maximum rates of evaporation obtained by WEAVER being three times and those by the reviewer at least twice those shown in Michigan; (2) the more humid climate exhibits a successional series much shorter than those in Washington and Indiana; and (3) GATES does not consider soil moisture conditions which would probably show all of his habitats to be decidedly mesophytic.

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[20] BOT. GAZ. **58**:232. 1914.

[21] CLEMENTS, F. E., Recent investigations on evaporation and succession. Plant World **20**:357–361. 1917.

[22] WEAVER, J. E., and THIEL, A. F., Ecological studies in the tension zone between prairie and woodland. Bot. Survey Neb. N.S. **1**:pp. 60. *figs. 38*. 1917.

[23] GATES, F. C., The relation between evaporation and plant succession in a given area. Amer. Jour. Bot. **4**:161–178. 1917.

In spite of this disagreement as to conclusions, however, GATES's investigation is to be welcomed as being carefully made and as adding to our knowledge of the moisture relations of various plant communities.—GEO. D. FULLER.

Germination.—LESAGE[24] has made a rather extensive study of the effect of various conditions and reagents upon the germination of seeds of *Lepidium sativum*. He finds a selectively permeable membrane surrounding the seed, as has been found for many other seeds. This is shown by the fact that the yellow pigment of the seeds diffuses out when the integrity of the membrane is destroyed by mutilation of the seeds or by treating them with dilute potassium hydrate solutions. The exosmose of the pigments occurs in hydrate solutions considerably more dilute ($\frac{1}{64}$ mol.) than those completely inhibiting germination ($\frac{5}{64}$ mol.). The data on the life duration of seeds, soaked in various concentrations of ethyl alcohol and aqueous solutions of salts followed by thorough washing in distilled water, are of great interest. Absolute alcohol did not injure these seeds after 4 years and 7 months soaking, and the life durations in various percentages are as follows:

94 per cent	2–3 months	33 per cent	2 hours
85 " "	50–90 hours	8 " "	4 days
75 " "	20 hours	5 " "	16 days
65 " "	6–7 hours		

If these data are plotted into a curve with the duration on the ordinates and the concentrations on the abscissae, the upward face of the curve is concave. A similar relation between toxicity and concentration holds for several salts that were studied. For NaCl and KCl solutions the highest toxicity (shortest life duration in the solution) was in 1–2 mol., and for NH_4Cl in 2–3 mol., higher concentrations proving less and less toxic as the concentration increased. For $NaNO_3$ the greatest toxicity lay between 2 and 4 mol., while for NH_4NO_3 it was between 1.25 and 6 mol. At the point of saturation, about 2 mol., KNO_3 had not reached its maximum toxicity. The seeds were not killed by 20 days' soaking in any concentration of Na_2SO_4, while $(NH_4)_2 SO_4$ showed its maximum toxicity at 2 mol.

The seeds still germinated after 4 years and 8 months soaking in petrol ether, but were quickly killed when soaked in ethyl ether. They germinated fairly well in moist air if it was saturated, but not at 98 per cent saturation. Temperature was an important factor here, 21° C. being the optimum. There is evidently a rest period in these seeds, for seeds one month old would not germinate in saturated atmosphere after 25 days, while 1-, 2-, 3-, 4-, and 5-year old seeds began to germinate after 3 days. Seeds that did not germinate after 5 months in saturated air still retained their vitality.

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[24] LESAGE, PIERRE, Au voisinage des limites de la germination dans les graines de *Lepidium sativum*. Rev. Gen. Bot. **29**:97–112, 137–157, 181–192. 1917.

Proper concentration of hydrogen peroxide proved to be a good forcing agent for such of these seeds as would not germinate readily, due to age or other causes. A 50 per cent aqueous solution of 8 vol. H_2O_2 completely inhibited germination, but 25 per cent and weaker solutions did not, but acted as forcing agents. While hydrogen peroxide hastened germination, it retarded the growth of the seedling.—WM. CROCKER.

Age and area hypothesis.—WILLIS[25] has recently advanced additional evidence to support his "age and area" hypothesis. Following his usual statistical method, he shows that the most widespread plants in New Zealand are those which reach outlying islands of the archipelago also. "There is no conceivable reason why ranging also to a few little islands should make a species more widespread in New Zealand, unless it be age, which has given them time to spread in New Zealand to the maximum degree."

In an accompanying paper the same author[26] strengthens his hypothesis by four additional pieces of evidence, arising from statistics on the following situations: the range of the orchids of Jamaica; the flora of Hawaii; the distribution of *Callitris* (Coniferae); the distribution of the ferns of New Zealand and Hawaii. "The endemic species (of ferns) show a much greater range than the endemic angiosperms, a result to be expected on my hypothesis, but contrary to what one would expect if endemics are dying out." In conclusion, the author points out that more care must be taken to consider geographical as well as structural relationship in forming genera and families.

It occurs to the reviewer to suggest that, in collecting data to support or discredit the age and area hypothesis, care should be taken that the plants considered are ecologically equivalent. The age and area hypothesis is founded on rate of distribution, and the latter certainly must vary as plants vary in their ecological status. In some of his more recent researches WILLIS has limited his consideration to plants of a given family. This should be more accurate than to consider any flora as a whole, for the plants within a given family are usually equivalent in their ecological status. This last, however, is not always true, so that the significance of some of the data given by WILLIS on distribution might sometimes be questioned. For example, it may be quite proper to say that widespread fern species are older than fern species of narrower distribution, but to state that because ferns are more widespread than angiosperms, the former are therefore older, is very questionable. Even if ferns were younger than angiosperms, the ease of spore dispersal might well render them more widespread than the latter.—MERLE C. COULTER.

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[25] WILLIS, J. C., The distribution of the plants of the outlying islands of New Zealand. Ann. Botany **31**:327–333. *fig. 1.* 1917.

[26] ———, Further evidence for age and area; its applicability to the ferns, etc. Ann. Botany **31**:335–349. 1917.

Fibers of tension.—JACCARD[27] has investigated anew the already frequently studied differences in the structure and composition of the wood on the upper and lower sides of dorsiventral branches of dicotyledonous trees, along with the stimuli producing these differences. In the upper side of such branches he frequently finds what he has termed "wood of tension" and "fibers of tension," while in the lower side he finds "wood of compression" and "fibers of compression." The fibers of tension are produced by the tension stimulus acting upon the cambium region. This stimulus may result from the weight of the branch or from bending due to other causes, as negative geotropism or torsion. Hence the fibers may occasionally appear on the lower side of the branch or even on vertical branches. They can also be produced by the mechanical bending of upright stems. The duration and intensity of the stimuli are important as in tropisms. There is also a summation of stimuli as in tropisms. He speaks of the formation of tension fibers as a purely physiological response, which has no hereditary or phylogenetic significance.

The wood of tension differs from the wood of compression in the following ways: more compact grouping of wood fibers with a corresponding reduction of vessels; more considerable development of medullary rays with their reserves; more regular grouping of the wood fibers; longer fibers with smaller lumina. The microchemical study indicates that the fibers of tension are made up of a combination of hemicellulose, pectin, and lignin. Fibers of tension are more general in summer than in autumn wood. Of the indigenous trees of France, *Tilia* only lacked fibers of tension, and of the introduced forms *Liriodendron Tulipifera* lacked them. *Rhus typhina* lacked while *R. cotinus* bore them. They are generally absent in such shrubs as *Lonicera*, *Ribes*, *Ligustrum*, *Viburnum*, and *Corylus*.—WM. CROCKER.

Ecological anatomy of leaves.—The variations in transpiration and in structure exhibited by the leaves of various forest trees have been studied by HANSON,[28] using material from isolated trees growing in the open. Light, evaporating power of the air, temperature, humidity, and wind velocity were measured at the south periphery and at the center of the crown of the same tree, the transpiration of leaves from these two positions determined by the use of potometers, the dry and green weights of equal leaf areas obtained, and finally leaves from the two situations were compared as to structure as exhibited, in cross-sections. All the environmental factors showed wide differences, which may be illustrated by taking those obtaining within and without the branches of *Acer saccharum*, one of the 10 tree species studied. Here the conditions within the crown compared with those at its south periphery were for

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[27] JACCARD, P., Bois de tension et bois de compression dans les branches doriventrales des feuilles. Rev. Gen. Bot. **19**: 225–242. 1917.

[28] HANSON, HERBERT C., Leaf structure as related to environment. Amer. Jour. Bot. **4**: 533–560. *figs. 21.* 1917.

light intensity 1.75:100; evaporating power of the air 1:2.3; humidity up to 100:84; wind velocity 1:2.2; and temperature from 1° to 2° C. higher at the latter position. Green and dry weights of leaves in the center of the crown were 46 and 38 per cent respectively of equal areas at the south periphery, while cross-sections showed differences of structure as great as those of weight, the average thickness of the centrally placed leaves being only 38 per cent of those at the periphery. The other species studied showed variations quite as interesting as those cited, the loss of water by transpiration showing a range of 3–12 times as much from leaves upon the south periphery as from equal leaf areas within the crown.

The investigation is particularly important in opening up a field of promising and almost unlimited possibilities in the study of structural response of aërial organs to measured variations in external factors.—GEO. D. FULLER.

Vegetation of Dutch Guinea.—Miss GIBBS[29] has added to her contributions to our knowledge of little known floras by exploring portions of the mountainous parts of Dutch N.W. New Guinea. The plant formations receiving most attention were the low mountain forest above 7000 ft., in which the dominant trees were *Quercus Lauterbachii*, *Podocarpus Rumphii*, *P. papuanus*, and *Phyllocladus hypophyllus*. These attained a height of some 16 m., with plenty of lianas, among which such ferns as *Gleichenia linearis*, *Nephrolepis acuminata*, and *Polybotrya arfakensis* were conspicuous. There were transitions to a mossy forest in which to the preceding trees there were added, among others, *Dacrydium novo-guineense* and *Librocedrus arfakensis*, making a remarkable aggregate of conifers, together with *Drimys arfakensis* and several Myrtaceae. Here a rich undergrowth of mosses, ferns, and herbaceous plants combined with an abundance of many epiphytic ferns and orchids. Locally in marshy localities there were found pure stands of the endemic *Araucaria Beccarii*. With increasing altitude the mossy forest decreased in height, although many of the same tree species persisted, with the addition of species of *Rhododendron* and several other ericaceous shrubs, as the mountain crest of 9000 ft. was reached. Here the trees were low and scrubby, the stand more open, and the growth of undershrubs more dense.

Miss GIBBS has recorded many interesting incidents of her trip and described less minutely other plant associations, but declares that she saw no forest that answered to the description of rain forest. Her collections showed 330 species, of which 100 were hitherto unknown; they included in addition 5 new genera.—GEO. D. FULLER.

Verbascum hybrids.—It has long been known that many hybrids occur in the genus *Verbascum*. FOCKE, SCHIFFNER, and others have made observations

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[29] GIBBS, LILIAN S., A contribution to the phytogeography and flora of the Arfak Mountains, etc. Dutch N.W. New Guinea. 8vo. pp. iv+226. *pls. 4. figs. 16.* London: Taylor and Francis. 1917. 12/6.

on these hybrids and KÖHLREUTER and GÄRTNER succeeded in getting hybrids experimentally. It is claimed that at the present time over 100 hybrids have been observed in this genus. BLOMQVIST[30] has made observations on *Verbascum* hybrids growing in the Swedish Royal Botanical Garden at Bergielund. Among the various species growing there, he discovered in 1908 eight individuals which he claims were hybrids in the following combinations: *V. nigrum*×*thapsus* (4), *V. nigrum*×*phlomoides* (1), *V. nigrum*×*lychnitis* (1), and *V. longifolium*×*speciosum* (2). His marks of identification were the sterile conditions and the intermediate forms of characters between two species. He made a special study of the two individuals which he calls *V. longifolium*×*speciosum*, since such a hybrid had not previously been discussed in botanical literature. These two examples show, in general, intermediate forms in the specific characters of the parents, except in the size of the flowers, which are markedly larger in the hybrids than in either of the parents. From his observations BLOMQVIST comes to a partial agreement with SCHIFFNER in that hybrids are intermediate in form between the parents; but he finds, as did DEVRIES, that while hybrids as a rule show such forms they may take on an exact resemblance to either parent or any transition form between.

The reviewer is of the opinion that, in the study of hybrids, simple observation does not suffice, since methods used in identification cannot give assurance of what hybrid is dealt with, and that such work should be checked up by experimentation.—HUGO L. BLOMQUIST.

Edible and poisonous mushrooms.—A generation ago Illinois took a very advanced position in the study of its fungous flora, and the late Professor BURRILL and his students have ranked among the foremost students of economic mycology in the country. The present publication,[31] paralleling what has been done in other states, is the first of its kind referring to an important, neglected, and much misunderstood branch of the same general subject, the fungi of Illinois which may be used as food or which should be known because of the danger which attends eating them. Structure, life history, and ecological relations are given ample consideration for an understanding of the fleshy fungi in more than their perfunctory recognition as fit or unfit for human food, and chapters are devoted to their cultivation, food value, or poisonous properties, and to the ways in which edible species may be prepared for the table.

The most practically useful part of the treatise, which should lead to the avoidance of accidents due to ignorance, and the utilization of large quantities of excellent food which now goes to waste, will be found in the clean cut keys and well written descriptions by which the several kinds may be known, and

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[30] BLOMQVIST S. G., *Verbascum*-Hybrider särskildt *V. longifolium*×*speciosum*. Acta Horti Bergiani **5**:1–10. *figs. 6.* 1909.

[31] MCDOUGALL, WALTER B., Some edible and poisonous mushrooms. Bull. Ill. State Lab. Nat. Hist. **11**:413–555. *pls. 85–143. fig. 1.* 1917.

in the large series of unusually good and well reproduced photographic illustrations by which the descriptions are reinforced. Although only a small fraction of the fleshy fungi of Illinois are included, the more important are considered, and the bulletin accounts for 61 edible and 9 inedible species.—W. TRELEASE.

Effect of copper sulphate.—JUNGELSON[32] has examined the effect that sterilization of seeds with copper sulphate solutions may have upon the plants developing from them. He used *Zea Mays* and soaked the seeds in 1 or 2 per cent copper sulphate 1–24 hours. Both intact and more or less mutilated seeds were used to give different degrees of contact between the salt and parts of the embryo. The treatment weakened germination, modified the chlorophyll of the young plant, and delayed vegetative development and flowering. It caused the formation of several types of ears and grains not found in the checks. These effects increased with the concentration of the solution, the duration of treatment, and the degree of excoriation of the seed. The treatment with copper gave no precise change in the plant, but rather a tendency to great variation in one or several of many directions. This tendency to vary was transmitted to the second generation. JUNGELSON believes that the degeneration of some excellent strains of cereals may have been due to excessive use of copper sulphate or other fungicides applied to seeds. He sees in this also the possibility of the origin of certain monsters that breed true.—WM. CROCKER.

Herbarium Amboinense.—A monument to American botanical activity in the Malay region is MERRILL'S "Interpretation of Rumphius's Herbarium Amboinense,[33] dedicated to the memory of CHARLES BUDD ROBINSON, JR., who lost his life in Amboina in 1913 while prosecuting studies toward its publication. RUMPHIUS, whose voluminous publication appeared about the middle of the eighteenth century, 50 years after his death, seems to have dealt primarily with the queer and the useful plants, and to have understood these and their relationships rather as the natives did than along the lines of modern taxonomy. Without its illustrations his herbarium would have passed into the category of efforts scarcely capable of correlation with subsequent work; with these, it has and will continue to hold a prominent place among publications on the Malay flora. The present "Interpretation" gives it a standing that should be lasting, provided care in the field, adequate linguistic preparation, scrupulous fidelity in weighing evidence, and an adherence to international rules of nomenclature can insure such a result for the work of one who today stands foremost in his knowledge of the Malay flora.—W. TRELEASE.

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[32] JUNGELSON, A., Sur des epis anormaux de maïs obtenus a la suite du traitement cuivrique de la semence. Rev. Gen. Bot. **29**: 244–248, 259–285. 1917.

[33] MERRILL, E. D., An interpretation of RUMPHIUS'S Herbarium Amboinense. pp. 595. Publ. no. 9. Depart. Agric. and Natural Resources, Bureau of Science. Manila: Bureau of Printing. 1917.

Endodermis and prothallium of Equisetum.—KASHYAP[34] has investigated the endodermis and prothallium of *Equisetum debile*. He finds that the endodermis is very unstable. At the nodes of the subterranean and aërial sterile shoots, and in the fertile region, the endodermis invests each vascular bundle, while in the internodes of the subterranean and aërial sterile shoots it surrounds the ring of bundles in two layers. These two rings of endodermis occasionally fuse, leaving islands of parenchymatous tissue. In the case of the prothallium, he discovered that if the spores are sown thickly, the prothallia remain small, develop only one growing point, and usually bear only one kind of sex organ. If the spores germinate at a distance from each other, the prothallia become very large and develop a meristem around the margin. It is somewhat remarkable that in this latter case the prothallia produce archegonia first and antheridia later.—J. M. C.

Variation in Picea excelsa.—A delayed volume of *Acta Horti Bergiana* contains a remarkable series of illustrations of variations in seedlings, leaves. and especially in the ovulate cones of *Picea excelsa*.[35] Most of the plates are double and many of them are beautifully colored, and the number of separate figures averages between 30 and 40 to a plate. The immense amount of variation shown in these figures doubtless would have induced many writers to multiply species. The present account consists of the figures and a good description of plates. There is scarcely a page of text. Even as it is, the illustrations are valuable as a record, and WITTROCK may give a full account later.—CHARLES J. CHAMBERLAIN.

Vegetation of Ohio.—Miss BRAUN[36] has studied the vegetation of Ohio as seen in the Cincinnati region, classifying the plant associations according to the physiography into the upland, slope, valley, and floodplain series. All the successions progress toward the mesophytic forest, the climax being either a forest of *Fagus* on the pre-erosion topography, or a mixed mesophytic forest upon the floodplains and in the ravines. She is of the opinion that this erosion climax, which resembles the forest of the southern Appalachians, is the more permanent and will eventually displace the pre-erosion climax beech forest. The report is well illustrated with photographs, maps, and diagrams.—GEO. D. FULLER.

Addisonia.—The fourth number of the second volume of this journal, with its "colored illustrations and popular descriptions of plants," includes the

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[34] KASHYAP, S. R., Notes on *Equisetum debile* Roxb. Ann. Botany **31**:439–445. *figs. 3.* 1917.

[35] WITTROCK, V. B., De *Picea excelsis* (Lam.) Lk., praesertim de formis suecicis hujus arboris. Pars I. Meddelanden om granen. Acti Horti Bergiani **5**:1–91. *pls. 1–23.* 1914.

[36] BRAUN, E. LUCY, The physiographic ecology of the Cincinnati region. Ohio Biol. Surv. **2**:(Bull. 7) 116–211. *figs. 58.* 1916.

following species: *Rosa* "Silver Moon" (a garden hybrid), *Dendrobium atro, violaceum* (New Guinea), *Centradenia floribunda* (Mexico and Central America), *Piaropus azureus* (Tropical America), *Solidago altissima* (Eastern United States), *Pentapterygium serpens* (Eastern Himalayan Region), *Freylinia lanceolata* (Southern Africa), *Anneslia Tweediei* (South America), *Crassula quadrifida* (Cape of Good Hope), *Aster cordifolius* (Eastern United States and Canada).—J. M. C.

Redwood distribution.—Investigating the factors limiting the distribution of *Sequoia sempervirens* in California, COOPER[37] has made measurements of rainfall at a considerable number of stations in the Santa Cruz Mountains, and has obtained evidence that heavy winter precipitation is necessary for the development of redwood forest. He also shows that this rainfall in itself is effective only when accompanied by abundant summer fog. In making the rainfall studies a type of rain gauge was used that makes possible the summation of precipitation for long periods.—GEO. D. FULLER.

Algae of Devils Lake.—MOORE[38] has published a preliminary list of the algae of Devils Lake, North Dakota, the chief point of interest being the alkaline character of the water, which has gradually increased with the diminishing size of the lake. All of the algae in the list were collected during August 1915, and comprise 47 species (29 Myxophyceae and 18 Chlorophyceae). No new genera or species were found, and all of the species were absolutely typical, with no indication of any effect of unusual environment.—J. M. C.

North American Flora.—The third part of volume 21 includes the Allioniceae (Chenopodiales) by STANDLEY. He defines 182 species in 26 genera, the large genera being *Abronia* (28), *Boerhaavia* (25), and *Allionia* (25). The new species are only 9 in number, but the author's name is associated with 71 additional species and with 5 genera.—J. M. C.

Soil toxins.—By very simple experiments PICKERING[39] demonstrates the effect of one plant on another through toxins. The simple technique and striking nature of the results are such as to suggest that similar experiments be introduced into all our laboratories.—GEO. D. FULLER.

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[37] COOPER, W. S., Redwoods, rainfall and fog. Plant World **20**:179–189. 1917.

[38] MOORE, GEORGE T., Algological notes. II. Preliminary list of algae in Devils Lake, North Dakota. Ann. Mo. Bot. Gard. **4**:293–303. 1917.

[39] PICKERING, SPENCER, The effect of one plant on another. Ann. Botany **31**: 181–187. 1917.

VOLUME LXV NUMBER 6

THE

BOTANICAL GAZETTE

JUNE 1918

SUCCESSIONS OF VEGETATION IN BOULDER PARK, COLORADO

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 238

W. W. ROBBINS

(WITH FOURTEEN FIGURES)

Introduction

This paper is concerned chiefly with the plant successions of the flood plains, lakes, and ponds of a mountain park. They culminate in a temporary meadow climax. Consideration is also given to the succession which begins on the xerophytic glacial gravels and passes through the characteristic and long persistent "dry grassland" stage also to a temporary meadow climax. There is also presented the interesting problem of the genetic relation of the meadow to the forests of aspen, lodgepole pine, and Engelmann spruce-balsam fir which border the open park. It should be stated that Boulder Park is typical, in its physiographic and vegetative development, of hundreds of such areas in the Rocky Mountain region.

Boulder Park is located in Gilpin County, Colorado, about 34 miles, in a straight line, west of Denver. The Divide of the main range of the Rocky Mountains is about 6 miles west; the Great Plains are about 18 miles east. Tolland, a small town near the middle of the Park, has an altitude of 8889 feet. The area falls within the montane zone (10).

Boulder Park was selected as the site for the University of Colorado Mountain Laboratory, the first session being held in the summer of 1909. Several papers (**11, 12, 19**) have been issued setting forth the facilities for field study at the Laboratory, but also presenting certain botanical features of the neighboring vegetation. Other papers dealing exclusively with the plant life of the Park and adjacent territory are referred to in this paper.

Topography and physiographic history

GENERAL.—The term "park" as used throughout the Rocky Mountain region refers to an open, flat, usually grassy area in the mountains. Such areas may be large, including 100 or more square miles; or small, containing only a portion of a square mile, and often possess a scattered growth of trees. Boulder Park is the broadened valley of South Boulder Creek. It is generally level, and through it flows the stream which is slowly working its way back and forth and producing well defined flood plains. The level portion of the park proper is bordered by steep slopes, the crests of which are 500–1000 ft. above the valley floor. The slopes have been burned over in large part, and exhibit various stages of the "burn succession," the most obvious of which are lodgepole pine and aspen. The climatic climax forest of Engelmann spruce-balsam fir is found in places. Some typical talus slopes occur. The country granitic rock is exposed in rugged outline in places, and may be observed in different stages of disintegration and decomposition, and in various stages of vegetative development. The building of the Moffat Railroad has created deep rock and gravel cuts, gravel and rock heaps and slides, often resembling talus and natural slides; likewise, the building of wagon roads has made many new areas whereupon secondary succession may be observed. The general topographic features of the Park may be seen by referring to figs. 1–3.

In Pleistocene times this area and many others in the mountains of Colorado were glaciated. The glaciers had their heads above timber line and moved down the valleys, leaving evidence of their action. The ice which was largely instrumental in shaping and modifying the topography of Boulder Park came from two sources,

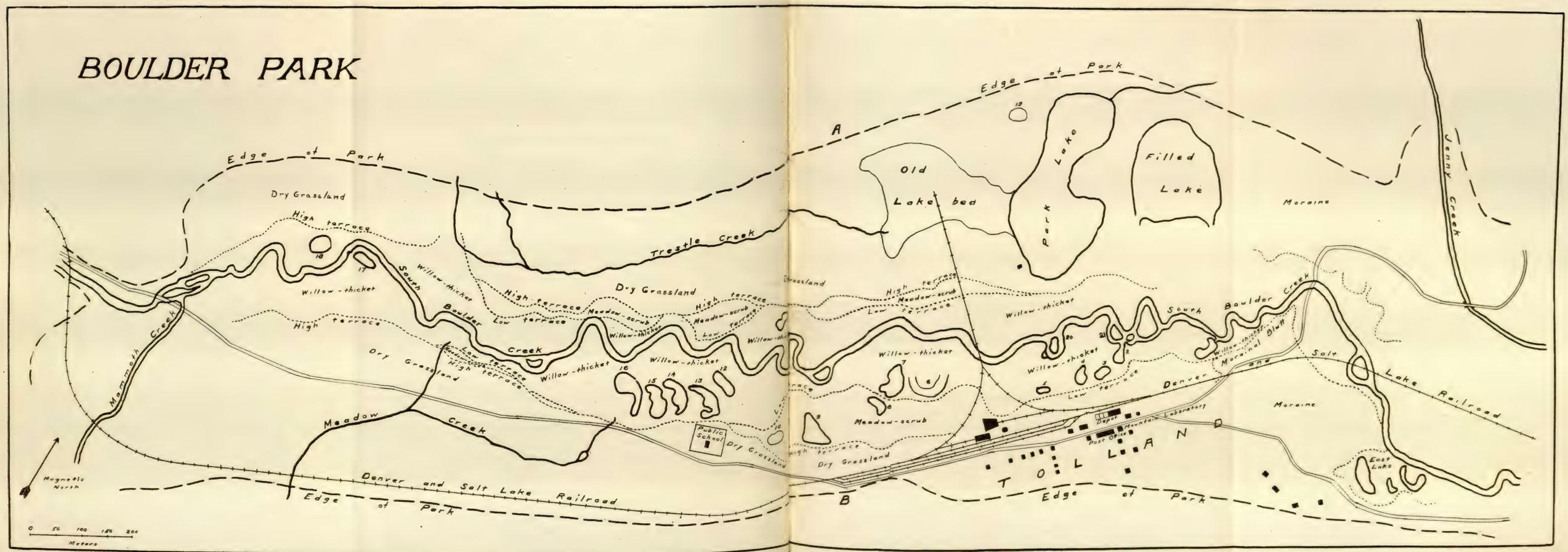


FIG. 1.—Map of Boulder Park (surveyed by [illegible]ODDS, W. L. BROSIUS, and W. W. ROBBINS)

South Boulder Canyon and Mammoth Gulch. The two bodies of ice no doubt met at the upper end of the Park and filled it to a depth of 400–550 ft., as is evidenced by the elevation of perched boulders on both slopes bordering the Park. Below Tolland is an area of hummocky topography typically morainal. The hummocks and the depressions between are strewn with rounded boulders, so much weathered that all traces of glacial scratches are obliterated. Post-glacial stream action has washed away great quantities of this terminal moraine. Lateral moraines join with the terminal and extend up the valley on the sides of the ridges. There is also a very wide and deep morainal deposit at the mouth of Mammoth Gulch. A comparatively small amount of it has been carried away. At the entrance of South Boulder Canyon, however,

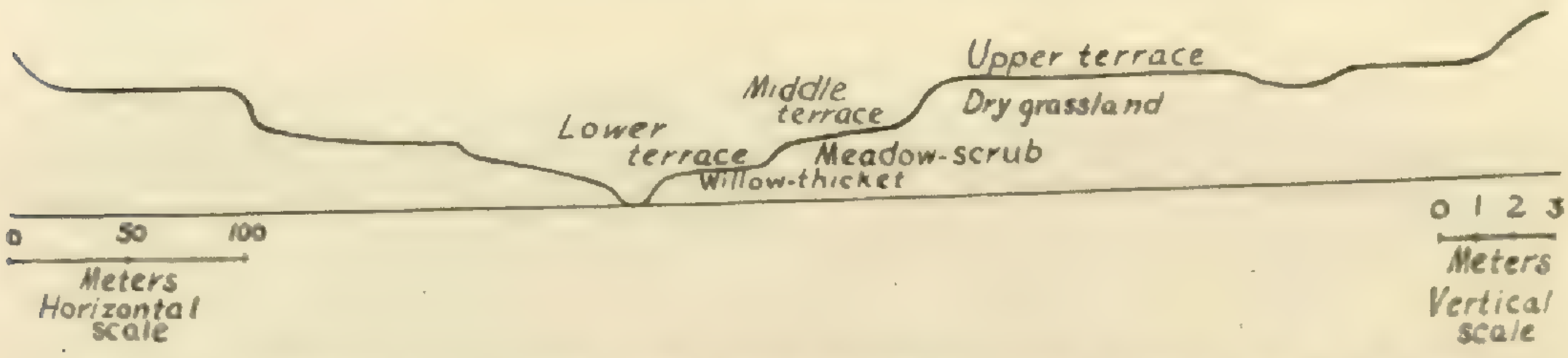


FIG. 2.—Profile of Boulder Park along line extending from *A* to *B* in fig. 1

but small remnants of moraine remain. This is undoubtedly due to the fact that South Boulder is a much larger stream than Mammoth, and since the retreat of the glacier it has carried away almost all of its moraine.

It has just been indicated that there are two large distinct deposits of morainal material in the Park: one below Tolland, the other at the mouth of Mammoth Gulch. They probably represent the terminals of two distinct glacial bodies of ice belonging to different periods of glaciation. In all instances where investigations (**1, 4, 7, 8, 9, 23, 26**) of the epochs of glaciation have been made in the western mountains, there have been two distinct epochs, and furthermore, in each case the earlier glacier extended farther than the later.

ORIGIN OF TERRACES.—The foregoing has been given in order to make clear the origin of the ponds and terraces which are such prominent features of the Park's topography. Figs. 1 and 2 show

that there are 3 main levels bordering the stream: (1) Low terraces, into which the present stream is now cutting. During high waters a portion of this may be inundated. Gravel is overlaid with a deposit of peat, ranging in depth from an inch or so to 3 or 4 ft. This level is covered with a willow thicket association in which the dominant forms are *Salix chlorophylla* Anders. and

FIG. 3.—View of Boulder Park looking west: James Peak at left and Continental Divide in background; glimpses of stream may be seen flowing through willow thicket association; note lighter colored patches of dry grassland; slopes are clothed with aspen, lodgepole pine, and Engelmann spruce-subalpine fir.

S. padophylla Rydb. (2) Middle terraces, meander terraces much older than the preceding. On the middle level the gravel is not overlaid with peat, except in a few places. The soil is a sandy and gravelly loam and 4–8 inches deep. The characteristic vegetation is meadow scrub in which *Salix glaucops* Anders., *Betula glandulosa* Sarg., *Dasiophora fruticosa* (L.) Rydb., and mesophytic herbs are dominant. (3) High terraces, which are composed of glacial gravels which have been worked over by the stream which issued from the

end of the retreating glacier. Typically, there is little accumulation of humus upon them. The vegetation is a "dry grassland."

The terminal moraine below Tolland undoubtedly acted as a dam to the stream coming from the glacial front, and for a long time the Park was the site of a lake. Subsequent to the period of deposition, the stream was lightened of its load and immediately began to cut into the terminal dam, which being of easily eroded material was quickly cut through. This resulted in a rapid drainage of the lake and the formation of a high terrace on each side of the stream issuing from the glacial front. The middle terraces are of stream origin.

ORIGIN OF LAKES AND PONDS.—With the exception of Park and Filled Lakes, all the natural ponds in the Park are of oxbow origin. Park and Filled Lakes are the largest and deepest. Their depth alone shows that they are not of oxbow origin. In the center of Filled Lake the peat is over 10 ft. deep. At no other point in the Park is there such a deep peat deposit. The relation these two lakes bear to the higher level shows that they were not formed during the deposition of the material composing this level. On the retreat of the first glacier two large ice cores were left on the valley floor. Hence, when the wash from the later terminal was brought down the valley it was deposited about the edges of these débris covered bodies of ice. The ice melted later, leaving the two lakes, Park and Filled.

Climatic factors

There are no extended climatic records for Boulder Park. ROBBINS (**22**) has shown the following average temperature and precipitation relations to exist in the "lodgepole pine forest zone" of Colorado, and from these a notion may be gained of climatic conditions in Boulder Park.

Mean annual temperature	34.9° F.
Mean winter temperature	18.4°
Mean spring temperature	33.4°
Mean summer temperature	53.6°
Mean fall temperature	38.4°
Average length of frostless season	67 days
Average date of last spring frost	June 20
Average date of first fall frost	September 9
Absolute annual range of temperature	104 days
Mean annual precipitation	25.53 inches
Mean annual snowfall	112.9 inches

During a portion of the growing seasons of 1909 and 1913, thermographs were run by members of the staff of the Mountain Laboratory. They show that the daily range of temperature may run high. This is particularly the case during clear weather. The daily minimum temperature is usually reached between 5:00 and 6:00 A.M., the daily maximum between 1:00 and 2:00 P.M. In 1909 the latest freezing temperature was June 22; in 1913 the temperature sometimes went down to freezing or below throughout July, and on August 1 of that year the minimum was 32° F. Afternoon showers of short duration during June, July, and August are common. Prolonged rains are infrequent. Although there is considerable snow, its accumulation on the high terraces, particularly, is largely prevented by their exposure to the sweep of winds from the west. There are large drifts of snow, however, in protected situations.

RAMALEY and MITCHELL (**18**) in 1909 determined the relative humidity at a number of Park stations. It varied on July 8 from 39 per cent on the north exposure of a railroad cut to 65 per cent in the lodgepole pine forest; on July 12, from 39 per cent in the railroad cut to 71 per cent in the forest.

Successions

FLOOD PLAIN SUCCESSION

Boulder Creek is a meandering stream with considerable cutting power. Along its course in the Park one may find shores of erosion, of deposition, and numerous oxbows in all physiographic and vegetative stages, and also well defined stream terraces. Hence there is an unexcelled opportunity here, as may be judged somewhat from a reference to fig. 1, to study succession on a mountain flood plain.

Two types of embryonic flood plains occur along Boulder Creek in its course through the Park: (1) those composed of well rounded boulders (cobblestones), averaging 2–6 inches in diameter, with a slight admixture of coarse gravel (fig. 4); and (2) those made of sand and silt (fig. 5). The former are initially xerophytic, the latter hydrophytic.

Shores of the cobblestone type may be partly under water during the spring or in wet seasons, but are usually bare in summer and

during dry years. The temperature extremes are great. Furthermore, the occurrence of flood-waters postpones the invasion of pioneers. The freshly exposed stones and gravel possess no vegetation. Algae which may have been clinging to rocks while submerged are killed on exposure to the sun. There is no lichen stage on the rock surfaces. The first plants gain a foothold in

FIG. 4.—Along South Boulder Creek: flood plain of cobblestones invaded by highly mixed plant community; note zone of *Carex variabilis* bordered outwardly by willow thicket.

the meager accumulation of fine sediment between the stones. *Agrostis hiemalis* (Walt.) B.S.P. and moss species usually initiate the succession. The individual grass plants form an interlacing, dense mass of fibrous roots which collect and hold sand and silt. These initial plants are followed by a highly mixed community composed of migrants from the sedge moor, willow thicket, meadow, and even dry grassland; in fact, there is no new habitat in the Park, except it is the roadside, where there is such a great number

of different species. The principal invaders are *Deschampsia caespitosa* (L.) Beauv., *Phleum alpinum* L., *Poa alpina* L., *Sporobolus brevifolius* (Nutt.) Scribn., *Carex variabilis* Bailey, *Salix chlorophylla* Anders., *S. padophylla* Rydb., *Sedum rhodanthum* Gray, and *Dodecatheon radicatum* Greene. The occurrence here of a depauperate form of *Erigeron eximius* Greene is interesting, as

FIG. 5.—Invasion of flood plain of sand and silt: note openness of vegetation, advancing clumps of *Agrostis hiemalis* and *Alopecurus fulvus*, and society of young *Salix chlorophylla* and *S. padophylla* shrubs.

is also the presence of such species as *Festuca ingrata* (Hack.) Rydb., *Rumex acetosella* L., *Arenaria Fendleri* Gray, *Sedum stenopetalum* Pursh, and *Dasiophora fruticosa*. In spite of the large number of species, the community is open. As vegetative development proceeds there is a reduction in the number of species and an increase in the number of individuals of the successful species, and increasing mesophytism of the habitat.

As is quite commonly the rule on flood plains, the first woody plants to gain a footing are *Salix* species. In this case the invaders are *S. chlorophylla* and *S. padophylla* (figs. 4, 5). After a few years a willow thicket is formed; at the present time extensive willow thickets prevail along the whole course of the stream on ground not far removed from the water level. The willow thicket has a peat deposit from a few inches to over 3 ft. deep. As has been indicated, the water level is near the surface at all times, and the association may undergo flooding in the early season.

In the series of successions starting with gravelly and stony stream banks, willow thicket is replaced by a meadow scrub. The presence of tall willows about a terrace lake in the Park has come to be looked upon as evidence of its oxbow origin. The dying out of tall willows in the drier portions of the willow thicket, the quite common presence of relicts of willow thicket throughout the meadow scrub, and the occurrence of small patches of meadow scrub throughout the willow thicket, are all evidences that willow thicket is being succeeded by meadow scrub. Such relicts are usually represented by a few tall *Salix padophylla* and *S. chlorophylla* shrubs, and in almost all instances such individuals possess many dead branches.

Meadow scrub attains its typical structure on the middle stream terrace. The characteristic shrubs are *Salix glaucops* and *Dasiophora fruticosa*, both of which are low forms as compared with those shrubs dominating the willow thicket. The herbs are those found in the herbaceous meadow of the Park. Meadow scrub commonly has a striking hummocky character. This is due to herbs building up about the shrubs. In places *Dasiophora* dominates the association. This shrub stands about 18 inches high, and the individuals usually 2 or 3 ft. apart. It has a considerable habitat range. In the progressive drying of the meadow scrub, it lags behind as a relict. It is, on the other hand, a common invader of the sedge moor.

The fact that meadow scrub on the middle terrace is laid on gravel indicates that the stream must have moved laterally rapidly on that level, thus giving little opportunity for the development of peat. At the present time the stream is swinging back and forth

across the valley at a comparatively slow rate, as is witnessed by the formation of peat on the recent levels.

Occasionally sedge moor may precede willow thicket on stream banks, and it is not at all uncommon to find stream banks of shingle remain xerophytic for a long period. The small isolated dry grassland patches throughout the willow thicket association are undoubtedly of this type.

Where the meander approaches its maximum curvature, the force of the stream on the inside of the curve is so slight that fine material is freely deposited. A good illustration of this is to be seen in oxbow 20 (fig. 5). The main current flows through the cut-off channel. A small portion of the stream with only slight carrying power still flows through the oxbow. It has built up a sandy and muddy stream flat. Such a habitat as this has a varied vegetative history. Usually, an association of *Eleocharis-Ranunculus* is the first to become established. This is the characteristic amphibious community of the Park. The principal species are *Eleocharis acicularis* (L.) R. and S., *E. palustris* (L.) R. and S., *Ranunculus reptans* L., *R. natans* L., *Allocarya scopulorum* Greene, and *Alopecurus fulvus* (L.) R. and S. *Eleocharis acicularis* builds a dense turf or mat. *Allocarya scopulorum* may also grow so thickly as to form a rather close growth over the soil surface. *Alopecurus fulvus* is a constant principal species of the community. *Eleocharis acicularis* often grows into several inches of water; such plants are sterile. However, by a slight lowering of the water level, the plants spread rapidly both by the underground parts and by seed, and in one season may make good headway toward reclamation of the mud flat exposed. *Eleocharis palustris* (fig. 6) finds its best expression in some of the oxbow lakes, especially those that have a flat, stony, or gravelly bottom and possess water only a part of the year. In oxbow lakes 8 and 9, for example, almost the entire area over which water stands, for a time at least, is covered with *Eleocharis palustris* and *Ranunculus reptans*. Rare associates are *Glyceria borealis* (Nash) A. Nels. and *G. grandis* Wats.

The *Eleocharis-Ranunculus* association is followed usually by sedge moor, in which *Carex variabilis* is the predominant species,

and this by a willow thicket of *Salix chlorophylla* and *S. padophylla*, or in certain instances the mud flat along streams may be invaded directly by *Salix* species, and still in other cases, especially where the soil is sandy rather than muddy, *Agrostis* is initial and is followed by a mixed community similar to that on more gravelly

FIG. 6.—Along shore of oxbow lake 9: at shore edge there is an almost pure association of *Carex utriculata;* bordered on water side by *Eleocharis palustris-Ranunculus* association; tall willows on farther side are relicts of willow thicket stage.

stream banks. This is replaced by willow thicket, which in turn gives way to a mesophytic grassland or meadow scrub.

Oxbow 20 (fig. 7) represents an oxbow in an early stage of formation. Some water is still flowing through the old channel (*egh*). The cut-off is clearly marked. From *c* to *d* a sand bar is being constructed and now almost reaches the water surface and extends from shore to shore. The outlet end of the oxbow will, of course, be the first to close. Then will follow the filling of the inlet, thus completing the formation of a closed body of water having the

shape of a bow. The shores of the newly formed lake have steep, vertical sides on the outside of the stream curve. On the inside

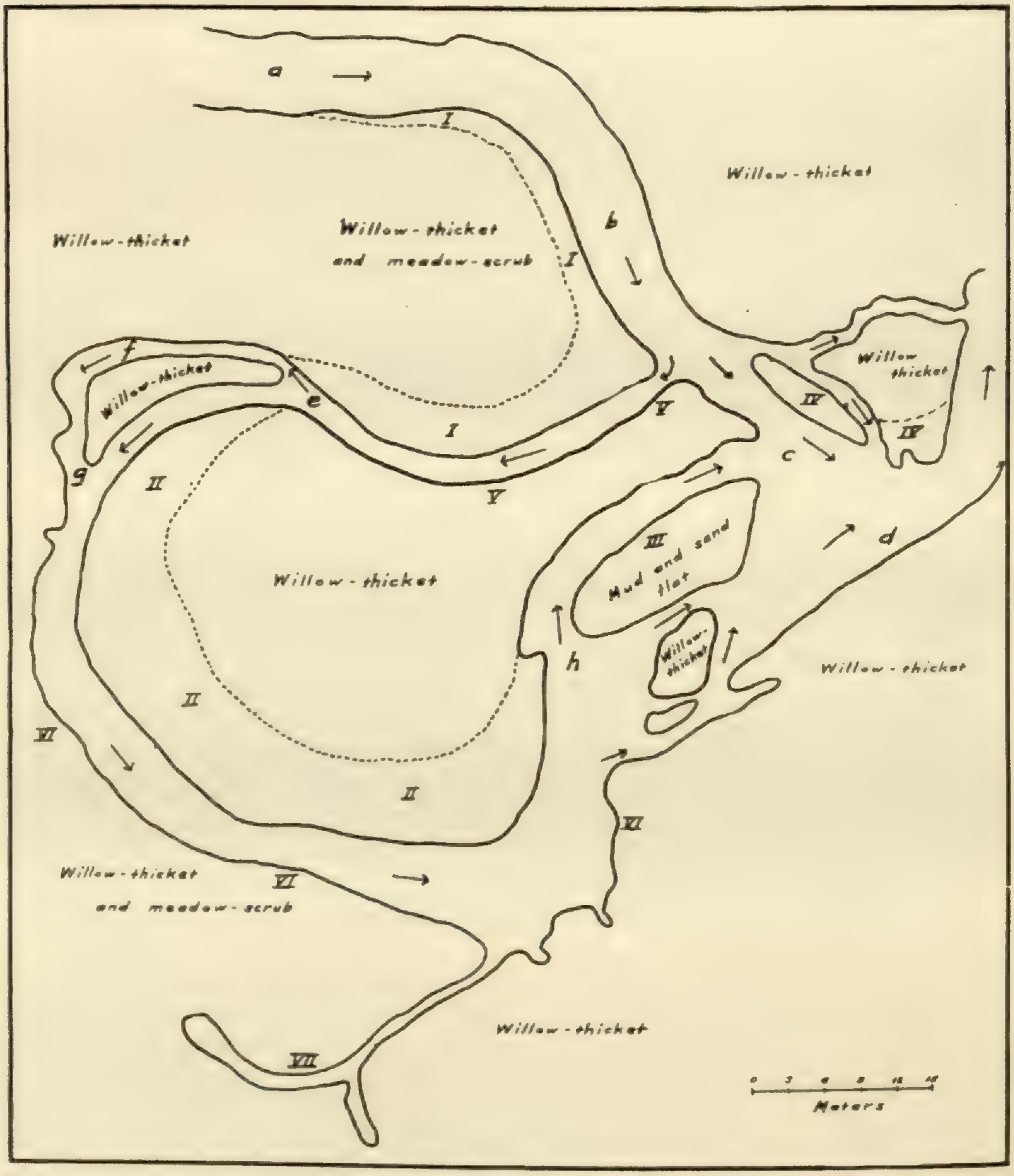


FIG. 7.—Map of oxbow no. 20: an early stage in the development of an oxbow lake; main stream occupies channel *abcd;* some water still flows through old channel (*egh*); from *c* to *d* a sand bar is being deposited; shore no. I, composed of sand, gravel, and boulders; at high water the strip may be covered; shore no. II, composed of gravel, sand, and fine silt; the bare soil is being invaded by a mixed association; shore no. III, a mud and sand flat under water a good part of the year; shore no. IV, cobblestone on which no vegetation has secured foothold; shores nos. V and VI, perpendicular erosion shores; "runs" of the kind shown at no. VII are common throughout the Park, being very narrow and with vertical walls.

of the curves there are gravelly, sandy, or muddy shores of deposition. The future history of this lake is now largely concerned with the activities of plants. In the developing of this oxbow lake *Callitriche palustris* L. and *Batrachium trichophyllum* (Chaix.) Bossch. are the first representatives of pond life. The main stream throughout the Park is too swift to allow the growth of any vegetation within it except algae, chiefly *Draparnaldia acuta* (Agardh) Kuetz. and *Prasiola mexicana* J. G. Agardh. These are attached to the rocks in the stream bed. They flourish only in swift running water. *Batrachium trichophyllum* and *Callitriche* have appeared in the still water back of the sand bar. Encroachment by the vegetation now starts in from all sides, and the area quickly comes to willow thicket. *Carex utriculata* sometimes becomes interpolated at the margin between willow thicket and open water. It is an important invader of these shallow oxbows. It is frequently succeeded by *Carex variabilis*, which is in turn followed by willow thicket. An oxbow that has had its connection with the main current severed usually passes through the same stages of succession found about lake shores.

Oxbow 3 is a somewhat different type from the preceding. The lake is shallow and has a muddy bottom, over which numerous small rocks are scattered. The orignal rock and gravel stream bed is thus still visible. The lake is free from water during the latter part of the season. *Alopecurus fulvus* is dominant on the muddy bottom. Associates are *Ranunculus reptans*, *Eleocharis acicularis*, and *Sparganium angustifolium* Michx. *Carex utriculata* is rapidly invading the *Alopecurus* society. Mixed with *Carex* is *Glyceria americana*, *Alopecurus fulvus*, and a great deal of moss. Moss often invades the *Carex utriculata* association, preparing a substratum upon which willow thicket may build more readily.

Oxbow 5 is a small and shallow pond which undergoes periodic drying. There is a well developed *Eleocharis-Ranunculus* association on the sandy bottom. It is being invaded by *Carex utriculata*, after which comes willow thicket.

Oxbow 6 exhibits a pond that is now almost filled with vegetation. A very small area of open water still remains. The lake was narrow and filled in a manner normal to gravelly or muddy shores,

that is, by the invasion of willow thicket. There is no vestige, however, of the first associations of these shores. *Carex utriculata* occupies the wettest part of the area. It is followed on all sides by the springy sedge moor of *Hypnum*, *Carex variabilis*, and *C. canescens* L. Here *Carex variabilis* is building upon the moss. The principal shrub succeeding *C. variabilis* is *Salix chlorophylla*.

Oxbow lakes 8 and 9 differ in a marked degree from all others in the Park. It will be seen that they are the only lakes of oxbow origin that occur on the middle terrace. Obviously they are physiographically much older than those of the lower stream terrace. They are very shallow and annually dry up. In spite of their age, they have not filled to any extent. Rock and coarse gravel, with but comparatively little finer material between, make up the pond bottom. This lack of plant débris is associated with periodic drying, and the exposure of the area to the winds. Late in a particularly dry season, the level bottom becomes dry and the strong winds blow away the material that accumulates. The chief associations over almost the entire lake bottom is an open one of *Eleocharis palustris* and *Ranunculus reptans* (fig. 6). *Glyceria borealis* and *G. grandis* are rare associates. About the shore edge *Carex utriculata* is slowly working inward. *Carex variabilis* or meadow scrub may come to the water's edge. A few clumps of *Salix chlorophylla* and *S. padophylla* at the edge are relicts of the old stream bank stage. Such individuals have numerous dead and dying branches.

East Lake (figs. 8, 9) is an old oxbow of South Boulder Creek, from which it is now separated by about 250 ft. The intervening area is a sedge moor alternating with willow thicket. Through this the lake outlet feebly flows. The old shore line of the creek is distinct. *Mertensia ciliata* (Torr.) Don. and *Senecio triangularis* Hook., typical streamside plants in the region, may be found sparingly in the willow thicket of the lake. *Salix chlorophylla* and *S. padophylla*, with the two associated herbaceous species, are relicts of a streamside flora. There is further evidence of the oxbow origin of East Lake. The stream cut into the terminal moraine and made a strong curve toward the southwest, working into its bank almost at right angles. As is happening at many places in the present

stream course, the shores were eroded and an inlet of considerable width and depth formed. We take it that the position of this is represented by the long tongue of sedge moor that extends from the lake edge to the meadow. Soil borings here show deep deposits of peat extending to the meadow.

At present, East Lake has a flat bottom and a uniform depth of about 1 ft. The bottom is of mud. The lake's development is

FIG. 8.—View of East Lake, of oxbow origin; beyond is portion of large terminal moraine.

natural and typical of an oxbow belonging to the lower terrace. The associations in and about the pond are arranged concentrically, particularly along the west and south sides. A small amount of *Batrachium* and *Callitriche* is found in the water. *Carex utriculata* makes a pure association chiefly along the west shore, where it is rapidly pushing out into the water. The plant is 1–2 ft. high and spreads by means of creeping rootstocks. Its typical habitat is still water not exceeding 1 ft. in depth. The amount of plant remains annually deposited by it is considerable. Furthermore, it

breaks wave action and thereby facilitates the accumulation of sediment between its closely crowded erect stalks. It is followed by the typical sedge moor, and this by willow thicket or meadow.

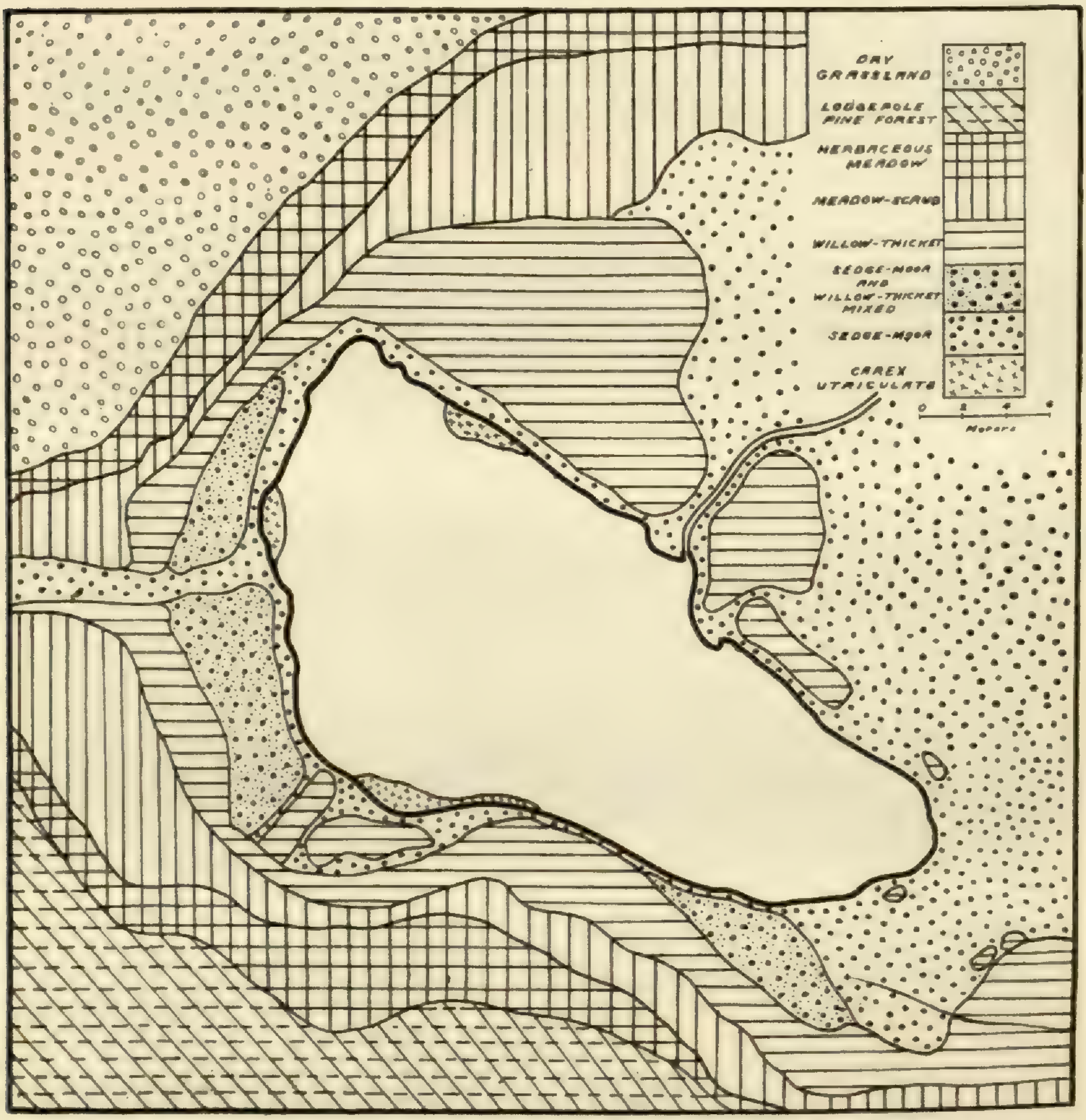


FIG. 9.—Map of East Lake, showing surrounding plant associations

Carex utriculata, however, is not the only agent in the invasion of the open water. Fig. 10 shows a section of the shore edge and sedge moor. It will be noted that there is a distinct elevated rim at the water's edge. This elevated rim is present almost entirely about the lake. Such a rim is commonly found along the streams, and is the result of stream cutting. Its occurrence about a lake may be taken as an evidence of its oxbow origin; not conclusively,

however, for the rim is also a feature of glacial lakes such as Red-rock (**20**) and Park, which are not genetically related to stream topography. In these it is no doubt formed by the sapping action of ice. Of course, stream action and ice action may be cooperative factors. At any rate, whatever its origin, once established the rim is maintained by vegetative building. At East Lake the rim about the edge has a mean height of about 16 inches. In texture it is a loose and spongy mass and consists of living and decayed

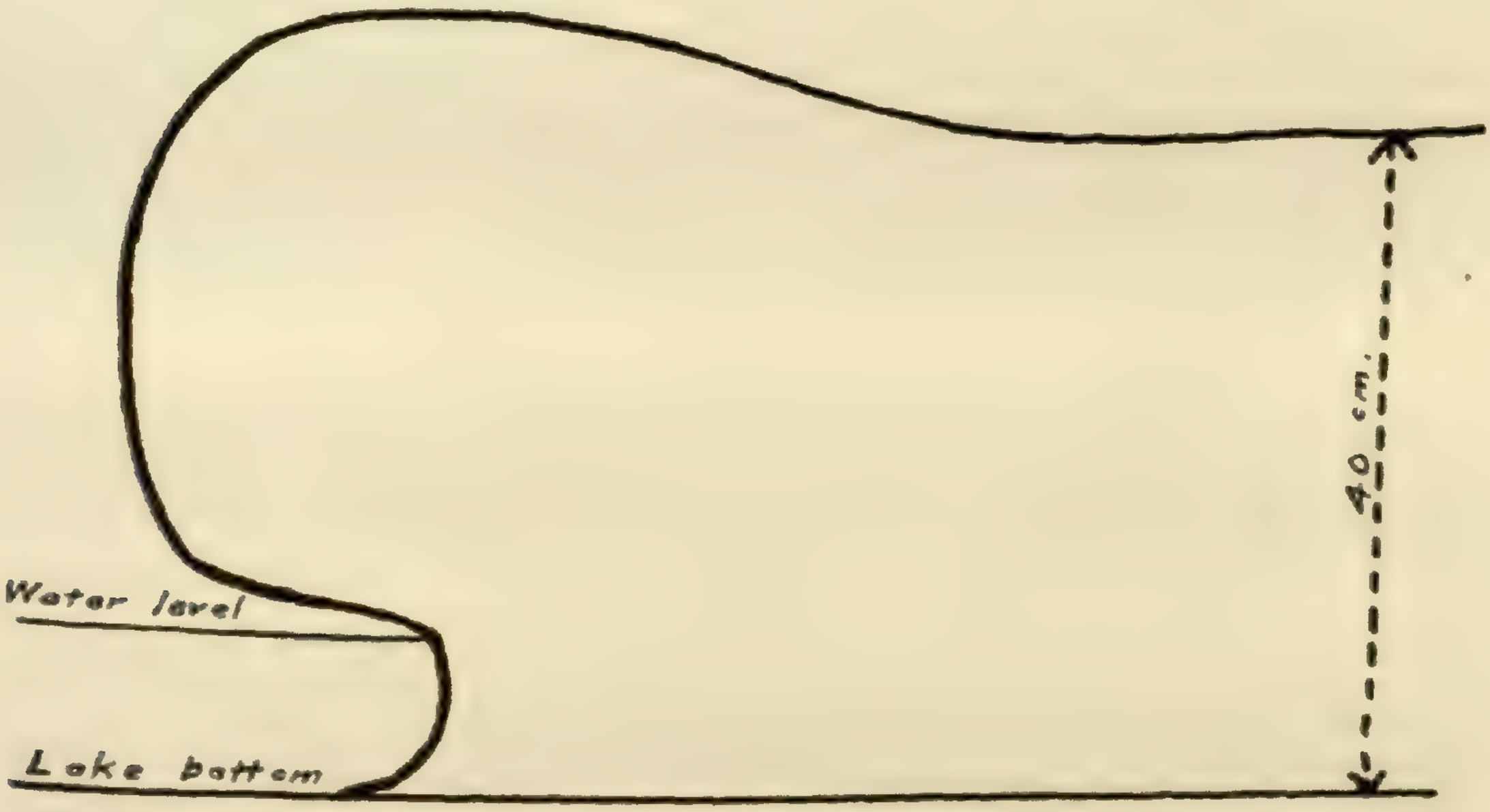


FIG. 10.—Section of "rim" and sedge moor at East Lake: rim which overhangs water has loose and spongy texture and consists of living and decayed plant material, largely masses.

plant material, largely mosses. Just back of the rim the soil is wetter, more compact, and the character of the vegetation somewhat different. Being actually drier than the moor a foot or so landward, it supports an assemblage of plants, many of which would scarcely be expected to grow at the water's edge. *Salix chlorophylla* and *Dasiophora fruticosa* are the important shrubs of the rim. The seeds lodge and germinate on the bare, more or less perpendicular, wall of the rim, and the young plants curve outward and upward over the water. Other characteristic rim plants are *Betula glandulosa*, *Sedum rhodanthum*, *Dodecatheon radicatum*, and *Poa leptocoma* Bong. The importance of moss in the building of the rim should be noted. As the rim slowly builds out over the

water, it sinks by its own weight, thus forming the flatter, lower, and more compact part just back from the edge. Willow thicket is invading the moor in many places. It is replaced by meadow scrub. At several points sedge moor passes directly into sedge moor, thus omitting the thicket and scrub stages of succession.

The principal species in the sedge moor of Boulder Park is *Carex variabilis*. It is a peat forming species. In reaction, the soil of the sedge moor is very slightly acid. The plants of the association stand close together. There is always an abundance of moss, which is of great importance in the building of peat. The sedge moor becomes marshy during the spring and early summer and after heavy rains. Then, the water aids in the packing down of dead sedge plants. The water table is always high and the soil water content high throughout the year. Stratification occurs to some extent. The following species form a ground layer: *Androsace subumbellata* (A. Nels.) Small, *Galium trifidum* L., *Crunocallis chamissonis* (Esch.) Greene, *Veronica serpyllifolia* L., *Alsine longifolia* (Muhl.) Brit., moss, and liverworts. *Caltha rotundifolia* (Huth.) Greene is an important component of the sedge moor. It is not a shade plant and hence does not do as well in the denser parts of the association as in more open spots.

Petasites sagittata Gray is prevernal in the sedge moor. *Caltha* is the characteristic species of the spring aspect (May 15–July 1). The summer aspect (July 1–August 15) is marked by a large number of sedges, grasses, and other herbs, most important of which are *Carex variabilis*, *Deschampsia caespitosa* (L.) Beauv., *Hierochloa odorata* (L.) R. and S., *Sedum rhodanthum* Gray, *Pedicularis groenlandica* Retz., and *Agrostis hiemalis* (Walt.) B.S.P. The appearance of gentians the latter part of August ushers in the autumn aspect (August 15–October 1). Chief of these are *Pleurogyne fontana* A. Nels. and *Gentiana plebeya* Cham. During the winter the sedge moor is a level expanse of withered shoots and leaves, chiefly *Carex*.

As compared with drier associations, the seasonal aspects of the sedge moor change slowly. The reason for this is partly the fact that *Carex* hides other forms growing within it, and furthermore to the actual paucity of species in this area as compared with drier

situations. More important, however, are soil, temperature, and moisture conditions. The maximum seasonal variations of soil temperature in typical associations during the summer of 1909 (13), as seen in the following table, will give some explanation of the rapidity of change in the seasonal aspects.

Sedge moor	7° F.
Willow thicket	8°
Meadow scrub	16°
Herbaceous meadow	20°
Dry grassland	24°

It will be noted from this that the sedge moor has the least variable soil temperature throughout the growing season. This condition is due for the most part to the amount and texture of the vegetative cover, and also is intimately related to the soil water content. Sedge moor vegetation screens the soil efficiently. Moreover, as a result of its high water content the specific heat of sedge moor soil is high and its conductivity of heat low. In the dry grassland, on the other hand, there is an absence of a dense vegetative covering. Here the soil has a low specific heat, due to its dryness, and its heat conductivity is great. Dry grassland heats up more rapidly and cools off more readily and to a greater depth sooner than either meadow or sedge moor. As regards soil temperature and soil moisture, the sedge moor shows less seasonal variation than either meadow or dry grassland. This condition appears to be correlated with the lack of marked seasonal aspects. Edaphic conditions within a community control the seasonal changes of the vegetative covering.

We have described the stages in the development of the flood plains of a mountain park. The oxbows and oxbow ponds are prominent features of these flood plains. Boulder and gravel shores or sand and fine silt shores are the initial habitats. They culminate in a temporary meadow climax. Two exceptionally distinct ages of flood plains are represented: a recently formed one now in the willow thicket stage, and an older one on the middle terrace in the meadow or temporary climax stage. A consideration of the fate of the meadow will be discussed later, after treatment of the glacial lake and dry grassland series of succession.

GLACIAL LAKE SUCCESSION

The origin of Park and Filled Lakes, the only glacial basins in Boulder Park, has been discussed. It was pointed out that these two bodies occupy the positions of two ice cores that were left on the valley floor on the retreat of the first ice mass. Immediately following the melting of these ice cores there was left a cold water lake with bare gravel and stony shores. Park Lake was formerly of much greater size; the limits of the old shore may be clearly seen on the west side of the present body of water. This filled area is now in the sedge moor stage of development, as is also Filled Lake. We may gain some idea of the early stages in the development of the shore vegetation by studying the alpine lakes which are found in abundance 6 or 8 miles west of Boulder Park. However, this difference exists: alpine lakes are comparatively well protected by cirque walls from wind effects, whereas those of Boulder Park are in the open. It is believed that this difference explains the tardy development of forest growth in the Park, and the maintenance of the temporary climax grassland.

In the lakes and ponds of Park Lake, algae are the only free floating plant life. Besides the numerous microscopic algae which constitute a portion of the plankton of these waters, *Mougeotia laetevirens* (A. Braun) Wittr. and *Spirogyra Weberi* Keutz. make up large floating masses along shores undisturbed by waves. *Anabaena flos-aquae* (Lyngbye) Breb. becomes conspicuous in late July when it appears as "water bloom" over the entire surface of the lake.

Sparganium angustifolium Michx. (fig. 11) forms a well defined aquatic community along the shore edge out to a depth of about 2 ft. It is of much importance in the aquatic successions. It grows equally well on a mud or gravelly bottom. A dwarf form occurs at the south of Park Lake on a low, flat area over which the water level fluctuates. Here the plants grow but a few inches high, and possess short, rather thick, leaves. Such plants mature fruit normally. *Callitriche palustris* L. is found in shallow water. It is most abundant where protected from wave action. *Batrachium trichophyllum* (Chaix) Bossch. is one of the first aquatics to secure a foothold in the ponds of the Park. It is the most

important aquatic in the filling process. *Potamogeton foliosus* Raf., *P. lonchites* Ruck., *P. alpinus* Balb., *P. interior* Rydb., *P. lucens* L., and *Myriophyllum spicatum* L. are other rather rare aquatics to be found here.

Aquatic plants play an important part in the life history of the lake. On the flat, mud shores the *Sparganium* association is

FIG. 11.—West shore at Park Lake; note *Sparganium* in shallow water, and zones of sedge moor and willow thicket.

immediately succeeded by the *Eleocharis-Ranunculus* community. This is well shown at the southwest shore (fig. 12). This shore is flat and gravelly or muddy, with a few small boulders scattered about. It is perennially covered with an inch or so of water up to about July 1, after which time it is a mud and gravel flat. Dwarf forms of *Sparganium angustifolium* flourish in this habitat. *Eleocharis acicularis* here, as elsewhere in such habitats, is the chief invader of the bare soil. Following close behind and upon pure tufts of *Eleocharis* come *Allocarya scopulorum* and *Alopecurus fulvus*, in the

order named. *Alopecurus* grows in caespitose clumps 3–6 inches in diameter. These tufts are the nucleus for the growth of such plants as *Epilobium Hornmannii* Reich., *Agrostis hiemalis*, and *Veronica serpyllifolia* L. Following the establishment of these herbs come *Carex variabilis*, *C. lanuginosa* Michx., *C. festiva* Dewey, *Deschampsia caespitosa*, *Phleum alpinum*, and *Poa leptocoma*. As

FIG. 12.—View of *Eleocharis-Ranunculus* association at southwest corner of Park Lake; community occupies a broad mud flat; note tufts of *Alopecurus fulvus*.

at East Lake, sedge moor may be succeeded directly by herbaceous meadow, the *Carex festiva* society being the first meadow community to become established.

Filled Lake is one of the most interesting features of the Park. This old lake bed is now in the sedge moor stage of development. The shore line is still quite distinct, made more so by the vegetative growth than by any topographic condition. Early successions now in operation at various places in the Park are undoubtedly similar to those which led up to the present sedge moor stage in Filled Lake.

The association immediately preceding the present one and the future changes are quite clear. The sedge moor is now dominated by *Carex variabilis* and *C. utriculata*, alternating and freely mixing. Obviously, *C. variabilis* has followed upon *C. utriculata*. Mosses

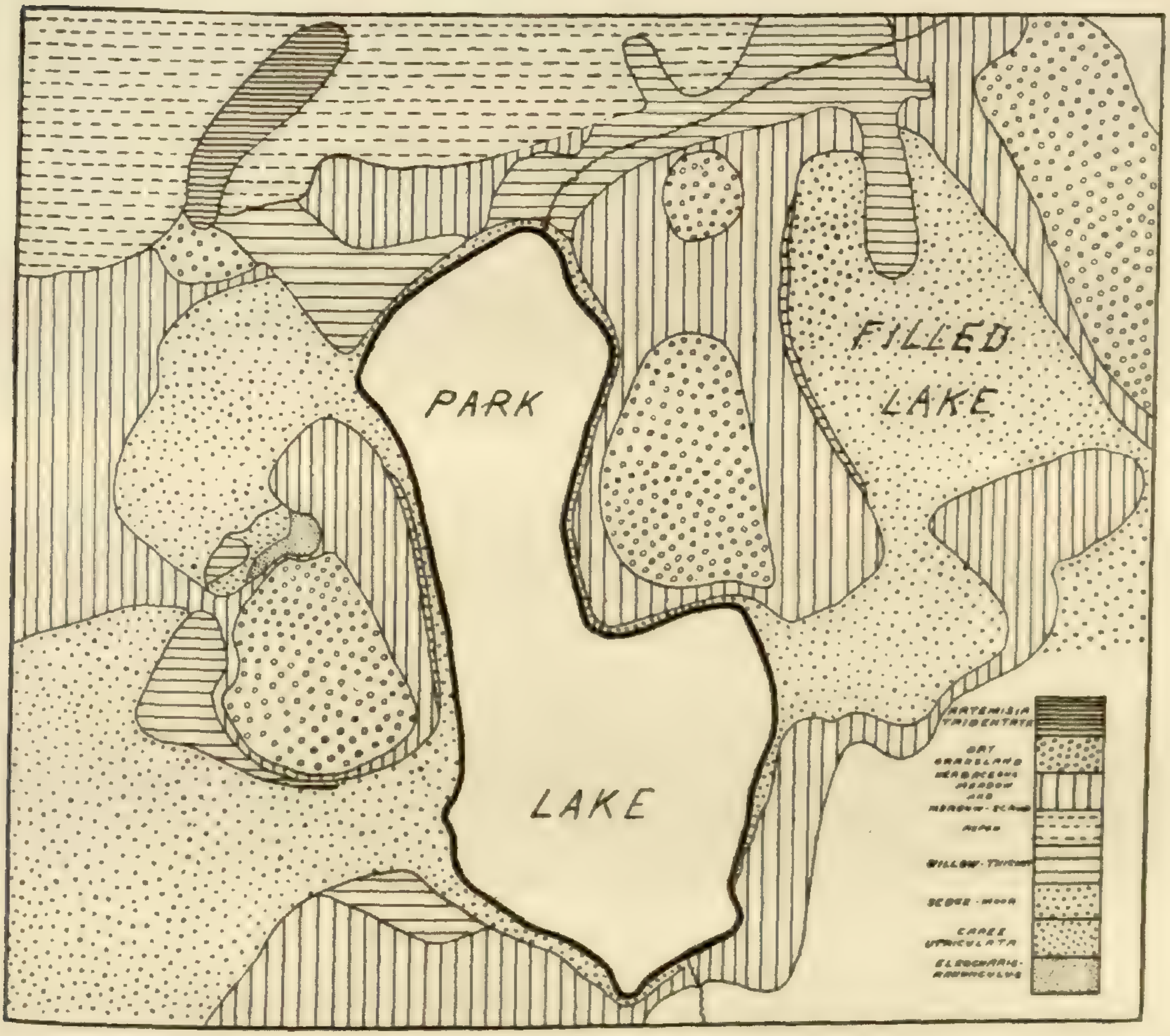


FIG. 13.—Map of Park and Filled Lakes

are an exceedingly important element in the building up of sedge moor.

If one stands at the old shore line and looks out over the flat, sedge-covered lake floor it is seen to be divided into two quite distinct parts: (1) the half nearer the outlet is lighter in color, due to the predominance of sedges, of which *C. utriculata* forms a good proportion; (2) the north half is darker, due to a pronounced admixture of *Deschampsia*, and a greater proportion of *C. variabilis* as compared with *C. utriculata*. The north half of the lake is drier.

This would be expected, since it is further removed from the outlet and is adjacent to the hill at the north, from which it has received considerable wash material.

Scattered throughout the sedge moor, and particularly in the upper half mentioned, are numerous clumps of vegetation. These are slightly elevated above the general level and vary from 1 to 3 ft. in diameter. The nucleus of a clump is usually a *Salix chlorophylla* shrub. This species is an early invader of sedge moor throughout the Park. Building in and around it are such early invaders as *Sedum rhodanthum*, *Alsine longifolia* (Muhl.) Brit., *Arabis hirsuta* Scop., *Cerastium occidentale* Greene, *Geum strictum* Ait., and *Dasiophora fruticosa*. The clumps may also originate about a

FIG. 14.—Ideal section at west shore of Park Lake

Dasiophora shrub or *Deschampsia* tuft. All the shrubs are young. Ring counts of *Dasiophora* show the large majority to be 13–15 years of age. *Salix* shrubs are older on the average. The sedge moor is rapidly being converted into meadow.

At the northwest shore of Filled Lake there is a shallow shelf extending outward from the shore line. The limits of this shelf were determined by making soil borings. These were simply used as a check on the determination of its limits by the vegetative covering. In fact, the presence of the shelf here was called to the attention by a rather marked difference in the vegetation as contrasted with that beyond. It is mentioned simply to illustrate transition conditions between sedge moor and meadow. Here *Deschampsia caespitosa* is predominant. Young *Dasiophora* shrubs are very uniformly distributed throughout. Sedges, relatively, are not an important component. Secondary species are: *Hierochloa odorata* (L.) R. and S., *Phleum alpinum* L., *Poa leptocoma*, *Cerastium occidentale*, *Alsine longifolia*, *Caltha rotundifolia* (Huth.) Greene., *Sedum rhodanthum*, *Geum strictum*, *Potentilla gracilis*, *Valeriana*

ceratophylla (Hook.) Piper, *Achillea lanulosa* Nutt., *Antennaria parvifolia* Nutt., and *Crepis perplexans* Rydb. The large number of characteristic meadow species will be noted.

The depth of the peat deposit in the lake was determined throughout. In the center it is over 10 ft. deep. From here the depth gradually decreases toward the shores. The rate of increase in depth may be judged by a set of borings made every 5 m. along an east-west line to the center of the area. Starting at the east shore this series shows depth (in cm.) as follows: 40–46–47–43–70–136–180–212–220–258–over 300.

Borings show that the lake has been filled almost entirely with the stems and leaves of *Carex*. The surface soil is loosely packed plant material, readily separated into layers, indicating seasonal deposition. The upper 6–8 inches are light brown in color; below this, the layers become darker and more compact. This soil exhibits a slight acid reaction.

It will be recalled that, at East Lake, *Salix chlorophylla* is a characteristic plant of the raised rim at the water's edge. A similar condition exists here. At the west shore there is a very distinct line of this shrub, on a more or less evident rim; at one time these formed a fringe at the water's edge. Back of this rim is a belt averaging about 20 ft. wide, clearly the old sedge moor of the lake shore. Beyond this is a meadow scrub, followed by herbaceous meadow, then dry grassland. The dry grassland is not the outcome of progressive drying of the meadow, as the zonation might suggest, but it represents a stage in a xerarch succession on the glacial gravel of the high terrace.

DRY GRASSLAND SUCCESSION

The rapid drainage of the lake which covered the entire park left a level, uniformly gravelly, area exposed to the drying and mechanical effects of the winds, and the extremes of diurnal and yearly temperatures. Lichens and *Selaginella densa* are the chief pioneers of the glacial gravels here. The latter is a mat former, and on the mats other plants gain a foothold. Its reaction upon the habitat, in holding the soil, adding humus, and retaining water, favors the entrance of such xerophytes as *Erigeron multifidus* Rydb.,

Sedum stenopetalum, *Potentilla concinna* Rich., *Carex stenophylla* Wahl., *Aragallus Lambertii* (Pursh) Greene, *Chrysopsis villosa* (Pursh) Nutt., *Comandra pallida* A.DC., *Arenaria Fendleri* Gray, *Artemisia frigida* Willd., and *A. canadensis* Michx.; simultaneously, there is an incoming of such grasses as *Muhlenbergia gracilis* Trin., *Danthonia Parryi* Scribn., *Festuca saximontana* Rydb., *Poa interior* Rydb., and *Koeleria cristata* Pers. There results a xerophytic grassland which has been designated "dry grassland." It is a persistent and long-lived plant community.

The dry grassland of Boulder Park has been the object of extended study by RAMALEY (**14, 15, 16, 17**). The association is preeminently one of coarse, gravelly, thin soils. Humus is conspicuously scarce. The soil temperatures run high throughout the vegetative season, and the soil water content low, at times falling below the wilting coefficient. The area is well exposed to the winds, and snow does not accumulate to any extent. RAMALEY has shown that 70 per cent of the most important dry grassland plants are shallow rooted, and that 33 per cent of them are rhizomatous; moreover, many of those which do not bear rhizomes have much branched caudices. Practically 91 per cent of the dry grassland plants are perennial. These facts point to the extreme xerophytism of the habitat.

The dry grassland is an open community; bare ground composes about 15 per cent of the whole area during the month of July. There is ample opportunity for seeds to find open territory; but the life of the seedling is a precarious one. There is a lack of soil water, droughts are frequent in summer, the transpiration rate is high, and there is a lack of winter snow cover. These conditions exclude the invasion of trees and many mesophytic plants.

Dry grassland has all appearances of being the ultimate vegetation throughout the Park, under present climatic and physiographic conditions at least. However, slowly but surely it is being invaded in places by meadow; a series of dry years may see the drying up of meadow, the fragmentation of plant parts, and their removal by wind, thus reinstating the dry grassland stage. The resultant is a slow encroachment of dry grassland by mesophytic grasses and other herbs. As has been indicated, if physiographic and climatic

conditions remain unchanged, the process of encroachment will be extremely slow. However, physiographic agencies are destroying the dry grassland habitat at a rate which exceeds that of biotic agencies. At many points the high terrace is being eroded by the stream, and invariably the flood plain temporarily culminates in meadow; again, débris is accumulating at the bases of slopes and in the depressions between glacial hummocks. On this fine grained and deeper soil, with its greater water retentiveness, meadow species become well established; hence it is seen that the combined activities of biotic and physiographic factors are resulting in the slow disappearance of the dry grassland and the establishment thereupon of a mesophytic grassland. FULLER (**6**) points out that whereas the hydrarch succession of Boulder Park is closely comparable to that of the Illinois prairie, the Park area exhibits a xerarch succession comparable to nothing found in Illinois.

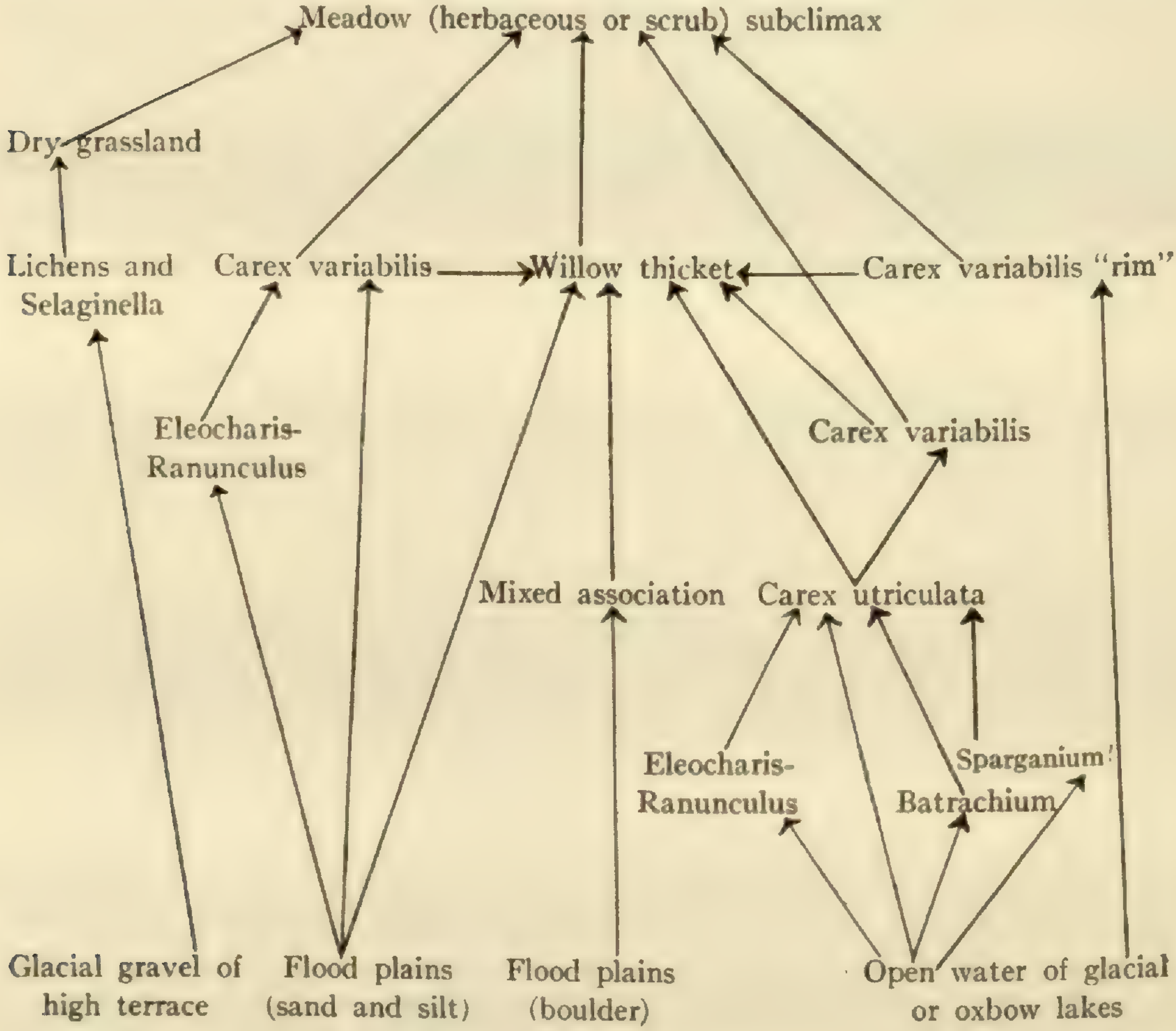
Two types of meadow are displayed in the Park which we have designated "herbaceous meadow" and "meadow scrub." The latter consistently occupies moister situations, and very frequently precedes herbaceous meadow in the succession.

The seasonal aspects and detailed structure of the meadow need not be entered into extensively here. REED (**21**) has given us a report of the chief meadow societies in the Park, together with a list of the meadow plants with their frequency and soil moisture index.

Carex festiva forms distinct meadow societies on the middle terrace and about the lakes. Where the slope of the lake shore is gradual, sedge moor immediately joins on to this society. Its chief associates are *Deschampsia caespitosa*, *Phleum alpinum*, *Potentilla gracilis* Dougl., *Poa Buckleyana* Nash, and *Poa pratensis* L. A conspicuous society of *Pedicularis Parryi* Gray occurs just outside the *Carex festiva* society in soil that is drier and more shallow. A quadrat census of the plants of the society showed the principal species to be *Potentilla gracilis*, *Astragalus alpinus* L., *Pseudocymopterus sylvaticus* A. Nels., and *Chondrophylla Fremontii* (Torr.) A. Nels. The most unobservant person would remark about the well defined limits of the *Pentstemon procerus* Dougl. society. It extends in a semicircle about the south flank of a low,

morainal elevation on the east side of Park Lake, and is also characteristic of glacial sinks. Grasses do not form a close growth, but other herbaceous species predominate. *Troximon glaucum* Nutt., *Potentilla gracilis*, and *Valeriana edulis* Nutt. are the principal associates. A society, the main representatives of which are

DIAGRAM OF PLANT SUCCESSION, BOULDER PARK, COLORADO



Erigeron macranthus Nutt., *Campanula Parryi* Gray, and *Eriogonum subalpinum* Greene, is characteristic of the meadow that immediately adjoins dry grassland. Associated species are *Galium boreale* L., *Achillaea lanulosa* Nutt., *Stipa Nelsonii* Scribn., *Poa interior* Rydb., and *Koeleria cristata* (L.) Pers.

Discussion

Based upon the water content of the initial habitat, the successions may be classified as hydrarch and xerarch. The hydrarch

succession involves the glacial lakes, and the flood plains with deposition banks of silt and sand; the xerarch succession involves the gravels laid bare by the rapid drainage of a glacial lake which at one time occupied the greater part of the Park, and the flood plains with shores of coarse gravel or shingle. The stages in these series lead to a temporary meadow climax (subclimax). The climax is reached much sooner by the hydrarch than by the xerarch series. In fact, much of the high terrace is now in the dry grassland stage, which under existing environmental conditions, incident to the topographical setting of the Park, promises to be long standing. However, there is ample evidence that even under these circumstances it is being slowly replaced by meadow. Moreover, the physiographic operations now in progress, namely, the erosion of Boulder, Meadow, and Trestle Creeks, and the accumulation of wash material at the bases of slopes, look toward the disappearance of the dry grassland habitat and the ushering in of meadowland.

The question now arises, are trees advancing upon the meadow? The forest associations bordering the Park are as follows: (1) aspen (*Populus tremuloides* Michx.), (2) lodgepole pine, (3) (*Pinus Murrayana* Oreg. Com.), and (3) *Engelmann spruce-subalpine fir* (*Picea Engelmannii* [Parry] Engelm.—*Abies lasiocarpa* [Hook.] Nutt.). Aspen often forms a fringe between the coniferous associations and the meadow of the open Park. This relation prevails throughout the Rocky Mountain region. Wherever the developmental series has led up to the meadow stage, however, as it has in Boulder Park, this stage bids fair to hold its ground against the invasion of trees, thus constituting a climax (subclimax) of long duration. The principal factor involved here is competition. It may occur to one that, although the competition of meadow species prevents the forestation of the open Park, there is nothing to prevent the dry grassland with its abundance of open ground being invaded by trees. In this connection it may be said that the exposure of the dry grassland to excessive evaporation as conditioned by wind, temperature, and the lack of a snow cover makes a situation in which trees find it impossible to get a start. The climatic climax of the region is a forest of Englemann spruce-subalpine fir.

In comparing the mountain lakes with those of the plains and lower altitudes generally, it is striking that those of lower elevations support the richer aquatic vegetation. The ponds of Boulder Park do not have many species commonly known as belonging to the water habitat. For example, there will be noted the total absence of species of *Lemna*, *Hydrocharis*, *Ceratophyllum*, *Utricularia*, *Riccia*, *Azolla*, and *Salvinia*, free floating species common at lower altitudes. Of these, several *Lemna* spp. and *Utricularia vulgaris* have been collected at elevations in Colorado as high as Boulder Park. Many submersed and emersed fixed species are not to be found here. Among such may be mentioned species of *Nitella*, *Isoetes*, *Naias*, *Elodea*, *Nymphaea*, and a number of *Potamogeton* spp. Several other species of *Potamogeton*, *Nymphaea polysepala* (Engelm.) Greene, *Isoetes Bolanderi* Engelm., *I. paupercula* (Engelm.) A. A. Eaton, and *Naias gaudalupensis* (Spreng.) Morong are reported from a few lower altitudes in Colorado.

The scarcity of aquatic plant life in the lakes and ponds of the Park is in part due to the coldness of the waters during a considerable portion of the year. Moreover, the marsh type of vegetation here is meager, and little shelter is offered to many free floating forms. The lakes and ponds in Boulder Park contain very soft water. No doubt the same is true of most high altitude lakes. Nearly all plains lakes, however, are rich in alkali salts; bicarbonates of calcium and magnesium, also of potassium and sodium, are quite universally present. A number of workers (**2, 5, 25**) have noted that waters rich in lime carbonates have a richer aquatic flora and fauna than soft waters. In the absence of free carbon dioxide, water plants may make use of the half-bound carbon dioxide of bicarbonates, chiefly those of calcium and magnesium, dissolved in the water. Undoubtedly the kind and quantity of dissolved salts in lake waters is an important factor in controlling vegetative development. In Boulder Park lakes and ponds the absence of these salts is quite likely a most important factor limiting the growth of algae and other submerged aquatics.

The total absence of *Scirpus*, *Typha*, and *Phragmites* reed swamps in Boulder Park will be noted.

SPHAGNUM BOGS.—Sphagnum moss is found in very small amounts here and there in the Park, but in no place is there any approach to the formation of sphagnum moor. Small sphagnum moors are occasionally found at higher elevations in heavily forested areas in northern Colorado, but never are they as well developed and characteristic as those found north and east in the United States.

For the optimum development of sphagnum, there must be abundant precipitation, slow evaporation from the surface, slow percolation and run-off of soil water, low temperature, and absence of drying winds. In only favored situations are such conditions found in Colorado. Boulder Park is a very unfavorable locality for the development of sphagnum moors. Here the drainage is generally good, the temperatures of both air and soil may run high, at least for a short period, many seasons are dry, and the winds are desiccating. In his description of the bog plant societies of northern North America, TRANSEAU (**24**) has selected 15 characteristic bog plants: *Menyanthes trifoliata*, *Dulichium arundinaceum*, *Comarum palustre*, *Scheuchzeria palustris*, *Eriophorum polystachon*, *Drosera rotundifolia*, *Sarracenia purpurea*, *Oxycoccus oxycoccus*, *Chiogenes hispidula*, *Andromeda polifolia*, *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Kalmia glauca*, *Betula pumila*, and *Larix laricina*. Of these, *Eriophorum polystachyon* is the only one found in Boulder Park, and it is rare. *Menyanthes trifoliata* has been found in a bog a number of miles north of Boulder Park.

The writer is indebted to Dr. H. C. COWLES, under whom this study was conducted, for his helpful suggestions and criticisms; to Professor FRANCIS RAMALEY for valuable advice and for laboratory facilities granted at the Mountain Laboratory for Field Biology (Tolland, Colorado); to Professor AVEN NELSON, who identified a large number of the specimens; and to Mr. A. S. HITCHCOCK for the identification of some difficult species of *Poa*.

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LITERATURE CITED

1. ATWOOD, W. W., The glaciation of the Uinta Mountains. Jour. Geol. **15**:790–804. 1907.
2. BIRGE, E. A., and JUDAY, C., The inland lakes of Wisconsin; dissolved gases and their biological significance. Wis. Surv. Bull. 22. 1911.
3. BRUDERLIN, KATHERINE, A study of the lodgepole pine forests of Boulder Park, Tolland, Colo. Univ. Colo. Studies **8**:265–275. 1911.
4. CAPPS, S. R., and LEFFINGWELL, E. D. K., Pleistocene geology of the Sawatch Range near Leadville, Colo. Jour. Geol. **12**:698–706. 1904.
5. CHAMBERS, C. O., The relation of algae to dissolved oxygen and carbon dioxide with special reference to the carbonates. 23d Ann. Rep. Mo. Bot. Gard. 171–207. 1912.
6. FULLER, G. D., A comparison of certain Rocky Mountain grasslands with the prairie of Illinois. Trans. Ill. Acad. Sci. **8**:1–10. 1917.
7. GWILLIM, J. C., Glaciation in the Atlin district, British Columbia. Jour. Geol. **10**:182–186. 1902.
8. HERSHEY, O. H., The relation between certain river terraces and the glacial series in Northwestern California. Jour. Geol. **11**:431–459. 1903.
9. JEFFERSON, W. D., A certain type of lake formation in the Canadian Rocky Mountains. Jour. Geol. **7**:247–261. 1899.
10. RAMALEY, FRANCIS, Plant zones in the Rocky Mountains of Colorado. Science N.S. **26**:642–643. 1907.
11. ———, Botanical opportunity in Colorado. Univ. Colo. Studies **6**:5–10. 1908.
12. ———, The University of Colorado Mountain Laboratory. Univ. Colo. Studies **7**:91–95. 1909.
13. ———, Northern Colorado plant communities with special reference to Boulder Park. Univ. Colo. Studies **7**:223–236. 1910.
14. ———, The amount of bare ground in some mountain grasslands. BOT. GAZ. **57**:526–528. 1914.
15. ———, The relative importance of different species in a mountain grassland. BOT. GAZ. 60:154–157. 1915.
16. ———, Quadrat studies in a mountain grassland. BOT. GAZ. **62**:70–74. 1916.
17. ———, Dry grassland of a high mountain park in Northern Colorado. Plant World **19**:249–270. 1916.
18. RAMALEY, FRANCIS, and MITCHELL, L. A., Ecological cross-section of Boulder Park (Tolland, Colo.). Univ. Colo. Studies **8**:277–287. 1911.
19. RAMALEY, FRANCIS, and ROBBINS, W. W., A summer laboratory for mountain botany. Plant World **12**:105–110. 1909.
20. ———, Studies in lake and streamside vegetation. I. Redrock Lake near Ward, Colo. Univ. Colo. Studies **6**:1. 1909.

21. REED, E. L., Meadow vegetation in the montane region of Northern Colorado. Bull. Torr. Bot. Club 44:97–109. 1917.
22. ROBBINS, W. W., Native vegetation and climate of Colorado in their relation to agriculture. Colo. Agric. Exper. Sta. Bull. 224:1–56. 1917.
23. SALISBURY, R. D., and BLACKWELDER, E., Glaciation in the Bighorn Mountains. Jour. Geol. 11:216–223. 1903.
24. TRANSEAU, E. N., On the geographical distribution and ecological relations of the bog plant societies of Northern America. BOT. GAZ. 36:401–421. 1903.
25. WESENBERG-LUND, Comparison of Scottish with Danish lakes. Revue Hydrobiol. 1:184–187. 1908.
26. WESTGATE, L. H., The Twin Lakes glaciated area, Colorado. Jour. Geol. 13:285–312. 1905.

QUANTITATIVE MEASUREMENT OF PERMEABILITY

WALTER STILES AND INGVAR JØRGENSEN

OSTERHOUT (8) has recently sought to explain the divergent results of some of his experiments and some of our own, on the basis of our confusion of permeability with absorption. It seems to us that any confusion that may have arisen is due largely to the different interpretations placed by different workers on such expressions as permeability in relation to complex systems like the cell. In this paper we discuss especially the meaning of the term permeability when it is used in a quantitative sense, and at the same time we take the opportunity of dealing with the points raised by OSTERHOUT in regard to the relation of his results and conclusions with our own. The term permeability may be classed with those expressions in current use in plant physiology which BARNES and LIVINGSTON (4) have described as cloaks for our ignorance. We may vaguely understand what is meant by the permeability of a membrane in regard to a particular substance, that is, its capacity for allowing the substance to pass through the membrane, although we may have no very clear idea as to how this takes place. In the case of the living cell, however, the matter is not so simple.

The nomenclature used in regard to the passage of substances into and out of the living cell has largely resulted from the work of DE VRIES on plasmolysis, and the theory derived from his results. It is a matter of common knowledge that as a result of the researches of DE VRIES (17, 18) and PFEFFER (9, 10), the plant cell came to be practically universally regarded as an osmotic cell, a solution surrounded by a semipermeable membrane, the plasma membrane, constituting the outer layer of the protoplast. On this view the permeability of the plasma membrane obviously means its capacity for allowing a substance to pass through the membrane. As plant physiology has developed, however, the realization of the complexity of the systems with which the plant physiologist has to deal has become more and more general, and it must be admitted that such a simple theory as that of DE VRIES will not afford a complete

explanation of the facts. Indeed, DE VRIES himself realized something of the complexity of the system, for he lays emphasis on the presence of two membranes which function in permeability phenomena, the outermost layer of the protoplasm, the plasma membrane, and the layer separating the rest of the protoplasm from the vacuole, the vacuole wall.[1]

In the simplest case of a plant cell immersed in a solution we have four phases: the external solution, the cell wall, the protoplast, and the vacuole; and in addition there are the limiting layers between these various phases which may have properties differing from those of either phase. We may represent such a system by the following scheme:

external solution	cell wall	protoplast	vacuole
phase boundary	phase boundary (plasma membrane)	phase boundary (vacuole wall)	

Again, in plant tissue intercellular spaces may also affect the results of investigations. Obviously in dealing with such a complex system the term permeability used in regard to the cell should only be used as a general expression to cover the various phenomena concerned in the passage of substances between living tissue and the external medium or between cell and cell in the living organism. It is in this sense that we have used the term permeability in our series of papers on these questions in *Annals of Botany;* we do not mean the capacity of substances to pass through any one particular phase of the system.

The permeability of living cells being then such a complex matter, it seems advisable not to use such expressions as "permeability coefficient," "measure of permeability," and "temperature coefficient of permeability," unless it is made clear what part of the system it is whose permeability is being considered. In our opinion the only legitimate use of such expressions is when they refer to the passage of substances into and out of the cell, or between one cell and another. Generally it is impossible by the methods of

[1] Cf. PFEFFER (11, p. 90): "In order to reach the cell sap a particle of water or dissolved substance must diosmose first through the cell wall and the plasmatic membrane which is closely applied to it, and finally pass through the internal limiting plasmatic membrane, which bounds the vacuole."

investigation at present available to analyze further the behavior of substances in passing through the various phases or across the boundaries between them. Hence, when we have used the term permeability in a quantitative sense we mean simply the capacity of a substance for entering the cell from the outside, or of passing out from the cell into the external medium, which are the phenomena with which we have so far mainly dealt. Generally we have not used the term permeability at all in a quantitative sense. Wherever possible it is much better to use the terms absorption or exosmosis, as the case may be, which have a definite unmistakable meaning and whose meaning does not depend upon an unproved and imperfect theory as does the term permeability as used by some writers.

In a paper (14) which appeared three years ago, we published the results of some experiments from which we concluded that the relation between time and absorption of hydrogen ions by potato cells was a logarithmic one, and that the temperature coefficient of this absorption was about 2.2. From this result it was pointed out that "the study of the effect of temperature on the absorption of the hydrogen ion would seem to indicate that this absorption is controlled by some chemical action in the cell, and is not the result of simple diffusion through the plasma membrane or of mere adsorption by the cell protoplasm." When therefore OSTERHOUT (8) says "it is evident, therefore, that the temperature coefficient observed by STILES and JØRGENSEN may be that of a chemical process involving the union of hydrogen ions with some constituent of the cell other than the plasma membrane," so far from contradicting our statement he is merely repeating our own conclusion in not very different words. When, however, he continues, "in which case it would have no bearing upon the problem of the nature of permeability," it would appear that he uses the term permeability, not in the general sense which we regard as the only legitimate one in which it can be used without qualification, but in a restricted sense, namely, the capacity of hydrogen ions for passing through "the plasma membrane (or other surface)." Against this restricted use of such a commonly used term as permeability we would enter a protest, as it rests upon a theory

which is unproved, which at best must be incomplete, and from which indeed many workers now dissent (FISCHER **1**, MOORE, ROAF, and WEBSTER **5, 6**). When, therefore, OSTERHOUT says of us that "they regard the temperature coefficient found by them as the temperature coefficient of permeability to hydrogen ions," he is completely misrepresenting our views on the matter. We never used the expression "temperature coefficient of permeability" for the reasons already mentioned, but if we had done so, we should certainly not have used the term permeability in the restricted sense in which OSTERHOUT appears to use it.

We may point out that OSTERHOUT's conclusion that we regard the temperature coefficient found by us as the "temperature coefficient of permeability" is based on the following assumptions: (1) that we "apparently reach the conclusion that 'the substance with which the acid reacts' is 'presumably the plasma membrane or some part of it'"; (2) that we support the view of PAULI and SZÜCS that the entrance of ions into the cell is due to the reversibility of a reaction between ions and the plasma membrane; (3) the title of our paper "The effect of temperature on the permeability of plant cells to the hydrogen ion." With regard to the first statement, we neither apparently nor in reality reached that conclusion. What we actually said was that our results indicated "that the quantity of substance with which the acid reacts, presumably the plasma membrane, or some part of it, remains constant as it does not influence the rate of the reaction." This is quite a different statement. We said "presumably the plasma membrane" because it could not be assumed that it was the plasma membrane;[2] it might be any part of the cell. It is quite an immaterial point; our argument holds equally whether the action takes place in the limiting layer or elsewhere in the cell.

Again, OSTERHOUT's second statement that we support the view of PAULI and SZÜCS is not founded on fact. We actually said, "this *suggests* that *either* the absorbing substance is present in such

[2] The term "plasma membrane" is another of those semimystical expressions whose use does not help in the elucidation of scientific problems. We prefer to use this expression in the way that LEPESCHKIN uses it, simply as meaning that part of the cell where the permeability phenomena are taking place. Compare our recent remarks on this term (**15**).

large quantity as compared with the acid that the amount changed is small in comparison with the total amount, *or* that the substance formed as a result of the absorption is broken down again almost as soon as formed. Such a view of the plasma membrane is held by PAULI and SZÜCS, who regard the entrance of ions into the cell as due to the reversibility of such a reaction between ions and the plasma membrane. *We feel, however, that more experimental evidence is required before such theories can be discussed adequately and with profit.*" It is extraordinary that anyone could see support for SZÜCS's view in that statement.

Finally, in the title of the paper the term permeability was used in its ordinary general sense, and in our opinion the title gave a reasonable representation of the contents of the paper, which should be its function.

For the reasons already stated we hold that that large body of workers who have included the absorption or exosmosis of dissolved substances among the phenomena of permeability are completely justified. OSTERHOUT'S statements, "the results obtained by these methods have been so largely misinterpreted," and "the principal difficulty lies in confusing permeability with absorption" seem to be due to his giving to the term permeability an indefinite and yet restricted meaning. It is unfortunate that he should not have realized that he and the writers he criticizes use the word permeability in a different sense; it is still more unfortunate that he should attribute to them his own use of the term permeability, and it is particularly regrettable that he should assume they mean the same things by "temperature coefficient of absorption" and "temperature coefficient of permeability" (in his sense, not theirs) when they carefully avoid such an expression as "temperature coefficient of permeability" on account of its indefinite meaning.

OSTERHOUT says that he himself used a method for determining the temperature coefficient of permeability which is free from the "objections" just discussed. We may now consider how far this statement is justified. He states that "by this method the electrical conductivity of living tissue was determined in such a way that it may be regarded as a measure of the permeability of the protoplasm." We propose therefore to discuss OSTERHOUT'S work under

three heads: (1) which part of the system it is, the permeability of which he intends to measure; (2) how far the values he obtains for the electrical conductivity of plant tissues are true measures of this conductivity; and (3) whether it is legitimate to assume that the electrical conductivity is a measure of the permeability.

In regard to the first question it is perhaps significant that when discussing the statements of the writers OSTERHOUT should speak of permeability in reference to the passage of substances through "the plasma membrane (or other surface)," while when discussing his own he should refer to the "permeability of the protoplasm." It is therefore not at all clear what it is that OSTERHOUT considers he is measuring, whether he is dealing with the whole cell content or part of it, or only the limiting layer of the protoplasm.

We come then to OSTERHOUT'S method of measuring the electrical conductivity of living tissues. The essential of this method (7) is that a pile of disks of *Laminaria* thallus is immersed in sea water or other medium between two electrodes. These are separated by a length of 20 mm. of sea water and the resistance between them measured. This resistance is called the resistance of the apparatus. The electrodes are then separated so that the roll of *Laminaria* disks is inserted between the electrodes in such a position that between each end of the roll of disks and the electrode is a length of 10 mm. of sea water. The resistance is again measured and the increase in resistance is taken to be the resistance of the tissue. Now whether the resistance of the tissue can be determined in this way depends entirely upon the form of the apparatus used, for the 20 mm. of sea water and the tissue must be strictly in series and there must be no surrounding conductor through which current might pass. As OSTERHOUT has never published any details regarding the arrangement of his apparatus, it is impossible to accept his results when their correctness is highly dependent upon the details of the experimental arrangement. Indeed, certain facts given in OSTERHOUT'S very inadequate description suggest an incorrect arrangement; for instance, why, if the sea water and *Laminaria* are arranged in series, should the resistance of 2 cm. of sea water be 305, while the resistance of 2 cm. of sea water plus a cylinder of sea water of the same transverse dimensions as the

tissue (5 cm. long) is only 392? No doubt an explanation of this is forthcoming, but it has not been given so far, and it will serve to indicate the necessity for a full description of OSTERHOUT'S apparatus and method before his conductivity measurements of tissues can be accepted by other workers.

Finally, there is the question as to whether the electrical conductivity of tissue can be used as a measure of permeability. Can it be assumed that the electrical conductivity as measured by KOHLRAUSCH'S method is really a measure of the permeability of the protoplasm to ions? We have already called attention (**12, 13**) to the fact that the conductivity of tissue is the resultant of the conductivity of a variety of different phases, and owing to the complex arrangement of these phases it cannot be assumed that the conductivity of the whole is the sum of the conductivity of each phase. HÖBER (**2, 3**), using a method which it is true is perhaps not above criticism, comes to the conclusion that the interior of the cell only contributes relatively slightly to the total conductivity. Moreover, OSTERHOUT neglects the fact that if the penetrability for ions increases, a necessary consequence of this may be increased diffusion between the external medium and the interior of the tissue, resulting in changes of concentration in the interior of the cell. Similarly, any change which altered the concentration or the distribution of free electrolytes in the interior of the cell would alter the conductivity. It may be, although we do not certainly know, that electrical conductivity gives a rough idea of the permeability of the cell; it is extremely unlikely that it gives numbers so exactly proportional to any kind of permeability that "temperature coefficients of permeability" can be calculated from them. Hence we consider it impossible to accept any of OSTERHOUT'S results obtained by his electrical conductivity method with *Laminaria* disks until (1) he makes clear what he means by permeability when this word is used in a quantitative sense; (2) he has given proof that his method does give values for the electrical conductivity of the tissue employed; and (3) he has produced evidence that the electrical conductivity of tissue can be taken as a measure of permeability in the sense in which he uses that word.

We should also like to raise two further points arising out of OSTERHOUT'S work. In the first place, we would point out that in

his discussion of our results, he would apparently apply conclusions derived from a brown alga immersed in a strong salt solution (about $\frac{N}{2}$), to potato tuber immersed in a dilute acid solution $\left(\frac{N}{1000}\right)$. Such a method of argument seems to us illegitimate. It is not to be accepted as a first principle that the permeability of every tissue, and permeability in regard to every substance or ion, will follow the same law. Secondly, we should like to caution in regard to temperature coefficients. When the temperature coefficient of the absorption of water by one tissue is found to be about 1.3 and by another tissue 3.0, as we have found with carrot and potato respectively, it should make one hesitate to draw conclusions as to the nature of a reaction from the magnitude of its temperature coefficient. That the temperature coefficient of the absorption of hydrogen ions by potato tissue is about 2.2 suggests, as we said previously, that the absorption is controlled by a chemical action, but without further evidence it is not more than a suggestion. This is forthcoming from the shape of the time-absorption curve and the fact that the absorption of hydrogen ions continues long after the concentration of hydrogen ion inside the tissue would be greater than that outside if no chemical action took place.

It must also not be forgotten that in cell problems we are dealing with a complex heterogeneous system, with probably a number of related and interdependent actions taking place, each one of which may have a different temperature coefficient. It would not be in any way surprising to obtain different coefficients for the same complex of processes with tissue that had had a different previous history, as we point out in a recent paper (**16**).

In conclusion, we should like to enter a plea for definiteness of statement and for the avoidance of semimystical expressions such as "permeability" or "plasma membrane" used in a quantitative and yet undefined sense. Above all, should be avoided the drawing of conclusions and the putting forward of theories on insufficient data.

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LITERATURE CITED

1. FISCHER, M., Œdema, a study of the physiology and the pathology of water absorption by the living organism. New York. 1910.
2. HÖBER, R., Ein zweites Verfahren, die Leitfähigkeit in Innern von Zellen zu messen. Pflügers Arch. Gesam. Physiologie **148**:189–221. 1912.
3. ———, Messungen der innern Leitfähigkeit von Zellen. Dritte Mitteilung. Pflügers Arch. Gesam. Physiologie **150**:15–45. 1913.
4. LIVINGSTON, B. E., A quarter century of growth in plant physiology. Plant World **20**:1–15. 1917.
5. MOORE, B., and ROAF, H. E., Direct measurements of the osmotic pressure of certain colloids. Biochem. Jour. **2**:34–73. 1907.
6. MOORE, B., ROAF, H. E., and WEBSTER, T. A., Direct measurement of the osmotic pressure of casein in alkaline solution. Experimental proof that apparent impermeability of a membrane to ions is not due to the properties of the membrane but to the colloid contained within the membrane. Biochem. Jour. **6**:110–126. 1912.
7. OSTERHOUT, W. J. V., Über den Temperatur Koeffizenten des elektrischen Leitvermögens im lebenden und toten Gewebe. Biochem. Zeitsch. **67**: 273–276. 1914.
8. ———, Does the temperature coefficient of permeability indicate that it is chemical in nature? BOT. GAZ. **63**:317–320. 1917.
9. PFEFFER, W., Osmotische Untersuchungen. Leipzig. 1877.
10. ———, Zur Kenntnis der Plasmahaut und der Vacuolen. Abh. Sächs. Gesell. Wiss. **16**:187–343. 1890.
11. ———, The physiology of plants (English trans.). Vol. 1. Oxford. 1900.
12. STILES, W., and JØRGENSEN, I., The measurement of electrical conductivity as a method of investigation in plant physiology. New Phytol. **13**: 226–242. 1914.
13. ———, Studies in permeability. I. The exosmosis of electrolytes as a criterion of antagonistic ion action. Ann. Botany **29**:349–367. 1915.
14. ———, Studies in permeability. II. The effect of temperature on the permeability of plant cells to the hydrogen ion. Ann. Botany **29**:611–618. 1915.
15. ———, Studies in permeability. IV. The action of various organic substances on the permeability of the plant cell, and its bearing on Czapek's theory of the plasma membrane. Ann. Botany **31**:47–76. 1917.
16. ———, Studies in permeability. V. The swelling of plant tissue in water and its relation to temperature and various dissolved substances. Ann. Botany **31**:415–434. 1917.
17. DE VRIES, H., Eine Methode zur Analyse der Turgorkraft. Jahrb. Wiss. Bot. **14**:427–601. 1884.
18. ———, Plasmolytische Studien über die Wand der Vacuolen. Jahrb. Wiss. Bot. **16**:465–598. 1885.

THE ZOOCECIDIA OF NORTHEASTERN UNITED STATES AND EASTERN CANADA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 239

B. W. WELLS

This summary is based upon a completed descriptive account[1] of the zoocecidia of the region studied, which is that phytogeographic region dealt with by GRAY'S *New Manual of Botany* (7th ed., 1908). The only similar general statement preceding this is that of FELT (4), who has presented some approximate figures from an entomological standpoint pertaining to American insect galls. The mite (Eriophyidae) galls were not included in his discussion.

Historical

Three local studies of zoocecidia have been made which deserve mention in a brief historical account. COOK (2) in 1904 published the description of 66 galls from Indiana. JARVIS (7) in 1908 presented a catalogue of the insect galls of Ontario, comprising 221 species. STEBBINS (10) in 1910 described 205 species of galls collected in the vicinity of Springfield, Massachusetts. A posthumous catalogue of 233 southern New England galls by THOMPSON (11) appeared in 1915, edited by FELT. This also included a summary of American Cynipidae galls, listing 350 species.

For the sake of comparison a short summary of the European work will be given. HAIMHOFFEN (5) in 1858 presented 350 as the number of zoocecidia for central Europe. SCHLECHTENDAL (9) in 1891 listed 1315 insect, mite, and nematode galls on the plants of Germany. KIEFFER (8) in 1901 published a synopsis of the zoocecidia of Europe. There also appeared the same year a more exhaustive study in DARBOUX and HOUARD'S (3) systematic

[1] The work contains the description of 792 nematode, mite, and insect galls; half of this number will be supplemented by illustrations. Keys to the galls on the various plant genera have been made, the plant genus constituting the unit by which the galls have been grouped.

catalogue of the zoocecidia of Europe and the basin of the Mediterranean, a work which in 1908 (supplement 1913) was expanded by HOUARD (**6**) into the largest systematic cecidological work in existence. This final general European work comprises the description of 1950 zoocecidia.

Basis and plan of work

The data from which the following summary is drawn were obtained during a period of 4 years, in which field studies in Connecticut, Ohio, and Kansas were supplemented by a thorough canvass of the highly scattered cecidological literature.

It may be of interest to mention the simple and, it is believed, practical scheme which has been followed in the arrangement of the 792 types described. The plant genus was made the unit under which the galls were grouped. This is in contrast to HOUARD'S plan; he used the species, a plan which necessitated a vast amount of repetition, since innumerable galls occur on more than one species within the genus. It is a striking fact that very few galls are found upon more than one genus. In the study of the galls of the northeastern United States, data concerning the plant species bearing the gall have been included with the descriptive material. To assist in locating the descriptions, keys were worked out for the genera having more than 6 or 8 species. A brief bibliography presenting the most important references was appended to each description.

The plant genera in the work have been arranged alphabetically. The galls under each genus have been aggregated according to the classification of the cecidozoons. It is thus evident that artificial classification has been pursued throughout. At the present time any classification of zoocecidia must be artificial. The morphological data available, particularly of an anatomical nature, are far too meager to make possible anything approaching a natural classification.

Summary of numerical data

In the case of all of the following figures presented, it should be understood that they are but approximations. So new is the field of systematic zoocecidology in America, and so incomplete and

unsatisfactory are the data in innumerable specific instances, that at the present time any generalizations of a numerical nature cannot be accepted as expressing the exact condition.

A tabulated statement of the 792 galls known from the northeastern quarter of the United States and eastern Canada, according to the cecidozoon orders and families, is as follows:

DISTRIBUTION BY ANIMAL FAMILIES

Nematoidea (Nematohelminthes)		Gelechiidae	3
Anguillulidae	2	Elachistidae	2
Acarida (Acarina)		Sesiidae	1
Eriophyidae	87	Tortricidae	2
Hemiptera (Insecta)		Unclassified	10
Aphididae	70	Diptera	
Psyllidae	6	Trypetidae	7
Jassidae	1	Itonididae	383
Coleoptera		Hymenoptera	
Cerambycidae	2	Chalcidae	2
Buprestidae	1	Tenthridinidae	13
Lepidoptera		Cynipidae	194
Tineidae	1		

As FELT has pointed out, the family containing the most gall makers is the Itonididae, embracing in our region 47 per cent of the gall biota. The Cynipidae follow with 37 per cent. The other families are represented by much smaller percentages, the Coleoptera being barely represented with 3 ill-defined galls.

The distribution of the galls (except nematode) by the plant families on whose members they occur is as follows. The families are arranged in the sequence given in GRAY'S *Manual*.

DISTRIBUTION BY PLANT FAMILIES

Pinaceae	13	Aristolochiaceae	2	Rosaceae	70
Typhaceae	1	Polygonaceae	2	Leguminosae	18
Gramineae	5	Chenopodiaceae	5	Euphorbiaceae	4
Cyperaceae	1	Nyctaginaceae	1	Anacardiaceae	10
Juncaceae	1	Portulacaceae	1	Aquifoliaceae	1
Liliaceae	9	Ranunculaceae	7	Celastraceae	1
Iridaceae	1	Magnoliaceae	2	Aceraceae	14
Salicaceae	60	Lauraceae	5	Balsaminaceae	3
Juglandaceae	64	Papaveraceae	1	Rhamnaceae	2
Betulaceae	18	Cruciferae	1	Vitaceae	20
Fagaceae	183	Saxifragaceae	5	Tiliaceae	7
Urticaceae	37	Hamamelidaceae	7	Malvaceae	1

DISTRIBUTION BY PLANT FAMILIES—*Continued*

Hypericaceae	2	Ericaceae	17	Labiatae	14
Violaceae	2	Primulaceae	1	Solanaceae	3
Cactaceae	1	Ebenaceae	2	Scrophulariaceae	2
Lythraceae	1	Oleaceae	6	Bignoniaceae	1
Onagraceae	1	Apocynaceae	1	Rubiaceae	3
Araliaceae	1	Asclepiadaceae	2	Caprifoliaceae	16
Umbelliferae	1	Convolvulaceae	1	Compositae	121
Cornaceae	11	Verbenaceae	3		

The striking fact brought out by this list is the extreme irregularity of the distribution. Many of the larger families have few or no galls, while on the other hand a few of the smaller families, particularly the Fagaceae, possess many cecidia. *Quercus* alone has 176 galls, of which 157 are cynipid types. FELT presents 277 as the approximate figure for the cynipid galls on the American oaks. The Cynipidae-Quercus situation in Europe as well as in America presents the most striking example of gall evolution within a single genus of plants related to a comparatively few (9 or 10) closely related genera of insects.

It is worthy of note that such large families as the Caryophyllaceae, Cruciferae, and Boraginaceae contain no gall-bearing species. The Umbelliferae possess but a single gall. The widely distributed tree species *Platanus occidentalis* does not bear any zoocecidia.

The problem in distribution on the plants presented by the preceding list is an exceedingly difficult one and probably cannot be answered on the basis of the physiological information at present available. This intimate and constant relation between specific insects and specific plants forms one of the most significant phenomena in the field of cecidology.

As far as data were obtainable, figures were worked out indicating the distribution of the galls on the plant parts, with the following result:

DISTRIBUTION ON PLANT PARTS

On leaf blade (of these 52 are "blister" galls)	427	On roots	12
On petiole (most of these occur also on blade)	47	On flowers	27
On stem (8 per cent of these occur also on the leaf)	208	From buds forming a rosette type	47
		From buds forming a solid concentric type	30

Slightly over half of the galls (53 per cent) occur on the leaf blade. This fact is of course related to the relatively large amount of embryonic leaf tissue exposed in the early stages of shoot development. In the cases of the stem, root, and bud galls numerous factors enter, but perhaps the most important is the factor of insect equipment necessary to place the larval cecidozoon in contact with the meristematic tissues.

Some figures pertaining to gall structure were obtained which are of interest. A few words of explanation are necessary before presenting the tabulation. Under the monothalamous galls were included those types which, so far as could be determined, are generally one-chambered, that is, the gall never is a structure constantly characterized by the confluence of the walls of two or more chambers as in the polythalamous condition. A few species are intermediate and were classified in the direction in which it was believed they leaned the more strongly. A number of galls, such as the erineum (hypertrophied epidermal cells) types, do not fall in either of the above categories and cannot be included in such a classification.

In those cases in which sufficient data were available, an attempt was made to study the galls on the basis of KÜSTER's division of cecidia into kataplasmas and prosoplasmas. By "kataplasmas" KÜSTER means those indefinite, indeterminate galls whose structure is developed through hyperplasia of embryonic tissue, the end product not becoming in its differentiation, orientation, and form of tissues fundamentally different from the normal plant part. "Prosoplasmas," on the other hand, are highly definite and determinate galls whose structure differs fundamentally from the normal plant, the tissues in their form and orientation characters constituting an aggregation of new qualities. These two groups intergrade, but the intergrading forms are relatively few in number and were classified according to what was believed to be the predominating condition. In all cases where data were not sufficient to pass judgment, the gall was omitted from the census.

Another set of figures presented is that based on KÜSTER's classification of galls into organoid and histoid types. An "organoid" gall is one in which an entire plant organ (leaf, stem,

internode, ovulary, etc.) as a unit suffers modification without a fundamental change in its morphology. The "histoid" galls are those more numerous types in which an entire plant organ is not involved, the gall being more or less definitely appendicular. This group includes all of the prosoplasmas and part of the kataplasmas.

DATA BASED ON NUMBER OF CHAMBERS

Monothalamous galls	408
Polythalamous galls	134
Non-chambered galls	67
Insufficient data to classify	183

The excessively large number of monothalamous forms is a fact related to the character of oviposition. If the eggs are habitually deposited in an aggregate manner, a polythalamous gall is almost certain to result, although there are striking exceptions to this. The great majority of larvae, however, begin their gall-making activity at sufficient distance apart to develop the common monothalamous types of cecidia.

KATAPLASMAS AND PROSOPLASMAS

Kataplasmas	395
Prosoplasmas	322
Insufficient data to classify	73

Viewed from an evolutionary standpoint, the kataplasmas represent the lower levels and the prosoplasmas the higher. That the latter have undergone a considerable expansion indicating relatively rapid progress in recent geologic time is evidenced by the relatively large number of prosoplasmas.

ORGANOID AND HISTOID GALLS

Organoid	215
Histoid	495
Insufficient data to classify	82

These figures have no special significance, perhaps, other than the indication of differences in the range of the gall stimulus. In the organoid types the stimulus is diffused over relatively large areas, inciting all of the tissues of one organ to hypertrophy and hyperplasia. In the histoid forms the stimulus only affects those tissues in a restricted area about the cecidozoon, these tissues responding in a definite and striking manner.

In addition to the above two tables KÜSTER has, in his classification of cecidia, furnished the basis for another table in his analysis of the prosoplasmas. These he divides into four groups: the leaf edge "roll" galls; the diverticulum or outpouching types; the "walled" (umwallungen) forms, whose walls grow up about the superficial larva; and the concentric (mark) cecidia whose larvae inaugurate gall formation from a point within the tissue. In the following list this classification was extended to include so far as possible the kataplasmas also, since a great many of these latter galls can properly be placed under some one of the preceding four groups. The 58 "rosette" and the 28 erineum types cannot be included.

NUMBERS OF VARIOUS GALL TYPES

Leaf edge "roll" types	32	Concentric types	
Diverticulum types		On leaves	145
Leaf or leaflet fold along mid-vein	19	On stems	184
Pouch types proper	109	On other parts	36
Walled (umwallungen) types	87	Galls unclassifiable in the above categories	86
		Unclassified through insufficient data	94

The factors entering into the production of these various kinds of galls are many; a full discussion of them cannot be presented here. Attention, however, should be called to the two main groups, namely, those which are related to the plant and those related to the cecidozoon. The diverticulum galls are, with few exceptions, only known from the leaf, particularly the blade, since this organ only is sufficiently free from stereome tissues to make possible the characteristic pouching out on the side opposite the cecidozoon. The walled and concentric types can occur on any part of the plant, the latter constituting a much larger aggregation than any of the other kinds. Oviposition within the plant tissue or a migration inward on the part of the larva is necessary for the production of the concentric type of gall. Even in these cases constituting the highest galls, plant factors can exert a modifying influence. The study of the relative importance of the two groups of factors entering into cecidium morphogenesis in specific cases is one of the most valuable and suggestive in the field of zoocecidology.

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LITERATURE CITED

1. CONNOLD, E. T., British vegetable galls. New York. 1902.
2. COOK, M. T., The insect galls of Indiana. 29th Ann. Rept. Dept. Geol. and Natural Hist. Indiana. pp. 801–867. 1904.
3. DARBOUX, and HOUARD, C., Catalog systematique des Zoocécidies de l'Europe at du Bassin méditerranée. Paris. 1901.
4. FELT, E. P., American insect galls. Ottawa Nat. **30**:37–39. 1916.
5. HAIMHOFFEN, G. R., Beobachtungen über die Menge und das Vorkommen der Pflanzengallen und ihre spezielle Verteilung auf die verschiedenen Pflanzengattungen und Arten. Verhandl. Zool.-Bot. Gesell. **8**:285. 1858.
6. HOUARD, C., Les Zoocecidies des Plantes d'Europe et du Bassin de la Meditteranee. 2 vols. Paris. 1909. Vol. 3, Paris. 1913.
7. JARVIS, T. D., A catalog of the gall insects of Ontario. 39th Ann. Rept. Ent. Soc. Ont. 70–98. 1908.
8. KIEFFER, J. J., Synopsis des Zoocecidies d'Europe. Ann. Soc. Entom. France. **70**:233–384. 1901.
9. SCHLECHTENDAL, D. H. R. v., Gallbildungen (Zoocecidien) der deutschen Gefasspflanzen. Zwickau. 1891.
10. STEBBINS, F. A., Insect galls of Springfield, Mass., and vicinity. Bull. 2. Springfield Mus. 1910.
11. THOMPSON, M. T., An illustrated catalog of American insect galls. Edited by E. P. FELT. Nassau, N. Y. 1915.

DIRECT ASSIMILATION OF ORGANIC CARBON BY CERATODON PURPUREUS[1]

WILLIAM J. ROBBINS

(WITH FIVE FIGURES)

Considerable attention has been devoted in recent years to the investigation of the assimilation by green plants of carbon in organic form. Attention has been directed to this phase of plant physiology because of the renewed interest in the relation of the organic compounds found in the organic material of the soil to the growth of green plants, and also because of the light which the result may throw on the question of the products formed in photosynthesis and of the function of various organic compounds in plant metabolism. A number of investigators have shown that higher plants may absorb and assimilate many organic compounds. In 1914 the writer began an investigation of the assimilation of organic compounds by the mosses. Circumstances made it impossible to complete the investigation. The results, however, show some facts and may prove suggestive to those who may continue the work.

SERVETTAZ (6) and VON UBISCH (7) have made observations upon the assimilation of organic carbon by the mosses. SERVETTAZ grew several species of mosses under sterile conditions on various solid and liquid media. Most of his work was done with *Hypnum purum*. According to SERVETTAZ the mosses when furnished with sugar or some other organic substance are able to live in the dark and become green slowly; but under these conditions they do not form starch and their increase is never important. Levulose, lactose, maltose, and saccharose when present at a concentration of 5 parts per 1000 favor development, but 2 parts per 100 are decidedly toxic. Dextrine, starch, and gum arabic at a concentration of 5 parts per 1000 retard development, but at 2 parts per 1000 favor it. *Hypnum purum* prefers the

[1] Published by permission of the Director of the Alabama Agricultural Experiment Station.

hexoses. Grown in the light in a mineral solution containing sugar, SERVETTAZ found that in 4 months *Hypnum purum* assimilated sugar, as given in table I.

TABLE I

Sugar	Original amount of sugar	Sugar used
Glucose	0.25 gm.	0.07 gm.
Levulose	0.25	0.065
Lactose	0.25	0.01
Maltose	0.25	0.005
Cane sugar	0.25	0.012

SERVETTAZ also found that peptone is assimilated by the mosses if present in concentrations below 2 parts per 1000. Inulin apparently is not assimilated.

The observations by VON UBISCH on the assimilation of organic carbon by the mosses were few. He grew several species of mosses in pure culture and noted the presence of large starch grains in the protonema of *Funaria hygrometrica* grown in the dark on a nutrient agar containing peptone and glucose. On the same agar lacking peptone and glucose the starch grains were very small.

Investigation

Although SERVETTAZ and VON UBISCH both obtained pure cultures from the spores in the capsules of various mosses, the moss used in this work was accidentally obtained in pure culture. It was found growing as a contamination in one of the culture vessels used by KNUDSON (3) in his investigation of the assimilation of organic compounds by the higher plants. Transferred to a nutrient agar it grew well. The protonema penetrated the soft agar and moss plants eventually were produced. It was identified as *Ceratodon purpureus* L. by Dr. A. L. ANDREWS of Cornell University, to whom the writer expresses his thanks.

USE OF ORGANIC CARBON.—Preliminary experiments showed that *Ceratodon purpureus* can assimilate organic carbon. In test tubes on a nutrient agar containing glucose the growth in the light was 4 or 5 times as luxuriant as on the nutrient agar lacking

glucose. The heavy dark green mat formed on the glucose agar is shown in fig. 1. This photograph was made 1 month after inoculation.

In solution cultures the utilization of the glucose was shown even more clearly. Fifty cc. of Czapek's nutrient solution for fungi (2) plus 0.1 gm. of calcium chloride per liter was placed in 125 cc. Erlenmeyer flasks. To some of the flasks 3 per cent glucose was added. All were sterilized and inoculated with the

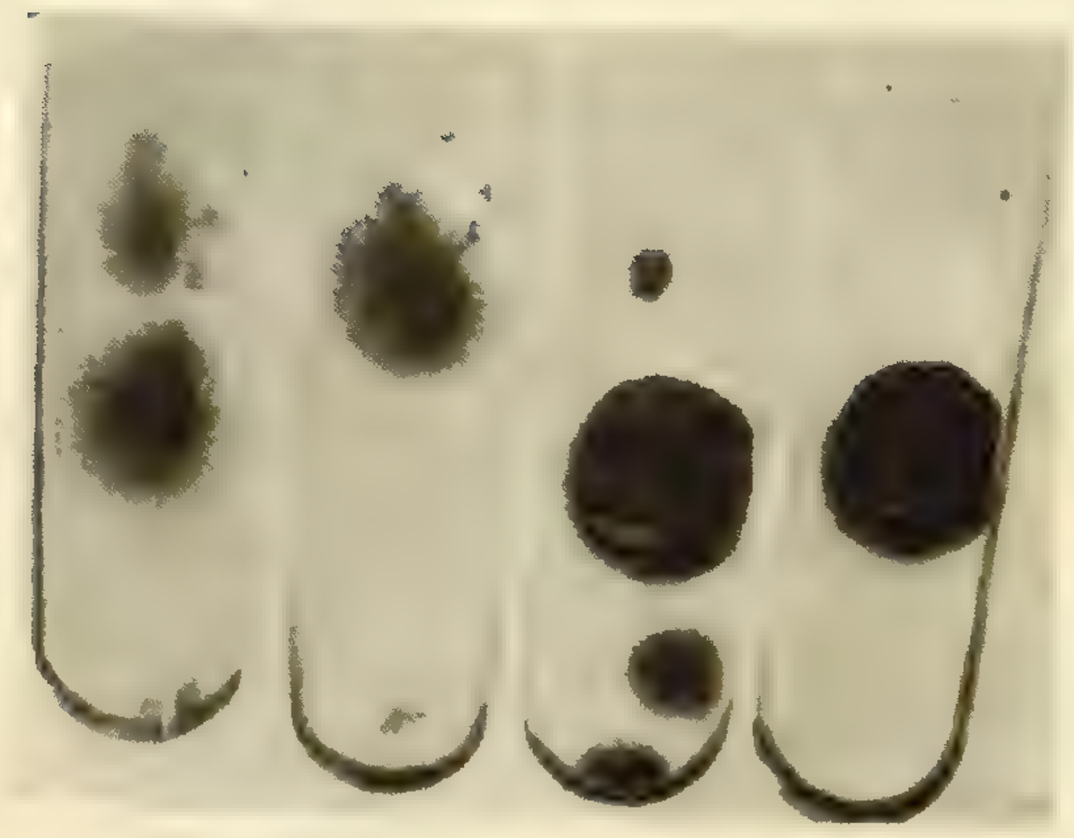

FIG. 1

FIG. 2

FIGS. 1, 2.—Fig. 1, *Ceratodon purpureus* grown 1 month in light on nutrient agar: 2 tubes to left contain no glucose; 2 tubes to right contain glucose; fig. 2, *Ceratodon purpureus* grown in dark for 1 month in modified Czapek's solution: flask to left contains 3 per cent glucose; flask to right contains no organic compound.

moss by transferring a bit of the protonema growing on agar in a test tube. Some of the flasks were placed in a north window and others in a dark cupboard. At the end of a month and a half it was found that in the light far more growth had occurred in the flasks containing glucose. In the glucose solution only protonema had developed; in the check young moss plants had been formed. In the dark no growth had occurred in the check, while the solutions in those flasks containing glucose were completely filled with a mass of dark reddish brown colored protonema (fig. 2).

AVAILABILITY OF DIFFERENT FORMS OF CARBON.—The culture solution used was one devised by MOORE for the culture of algae,

and is described by REED (5). The carbon compounds were all Merck's products. Dextrose, pure, "Mulford" and Schering's levulose were also used in repeating some of the experiments.

Sufficient of the organic compound was added to make a concentration of 0.1 mol. The culture vessels were 125 cc. Erlenmeyer flasks, containing 50 cc. of solution. Those sugars, such as cane sugar, which could be hydrolyzed were sterilized in an Arnold sterilizer and tested for hydrolysis before use. After sterilization

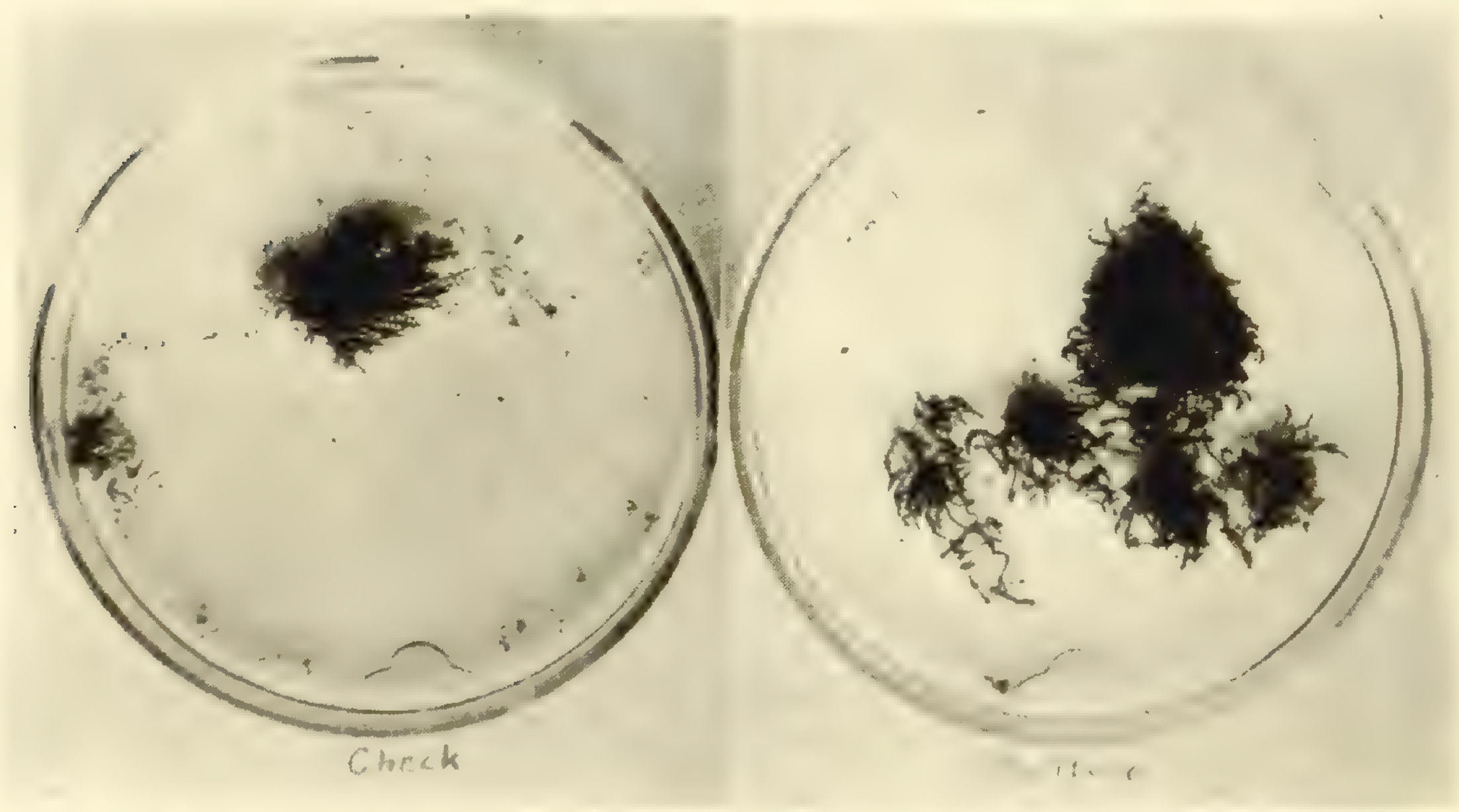

FIG. 3.—*Ceratodon purpureus* grown in nutrient solution in light for 2.5 months: on left grown without organic compound; on right grown in 0.1 mol. maltose.

the flasks were inoculated, as previously described, with the moss protonema. The moss was grown for 2.5 months in the presence of each carbon source in triplicate culture both in the light and in the dark.

In the dark the moss grew in the levulose, glucose, cane sugar, maltose, galactose, and lactose solutions. The amount of growth was greatest with levulose as the source of carbon. In the galactose and lactose solutions the growth was very slight. No growth, save a slight lengthening of the filaments of the original material, occurred in the check, nor in the presence of mannite, glycerine, or starch. In all cases in the dark the growth consisted of protonema. No moss plants were produced. The protonema, instead of having

the familiar yellow color of chlorotic higher plants, was a dark reddish brown.

By the use of iodine starch was demonstrated in the protonema grown in the levulose, glucose, cane sugar, maltose, galactose, and lactose solutions. The protonema grown in the levulose solution contained the most starch. At the end of the experiment it was found that the cane sugar was completely inverted. The use of Barfoed's solution and the osazone test failed to demonstrate the

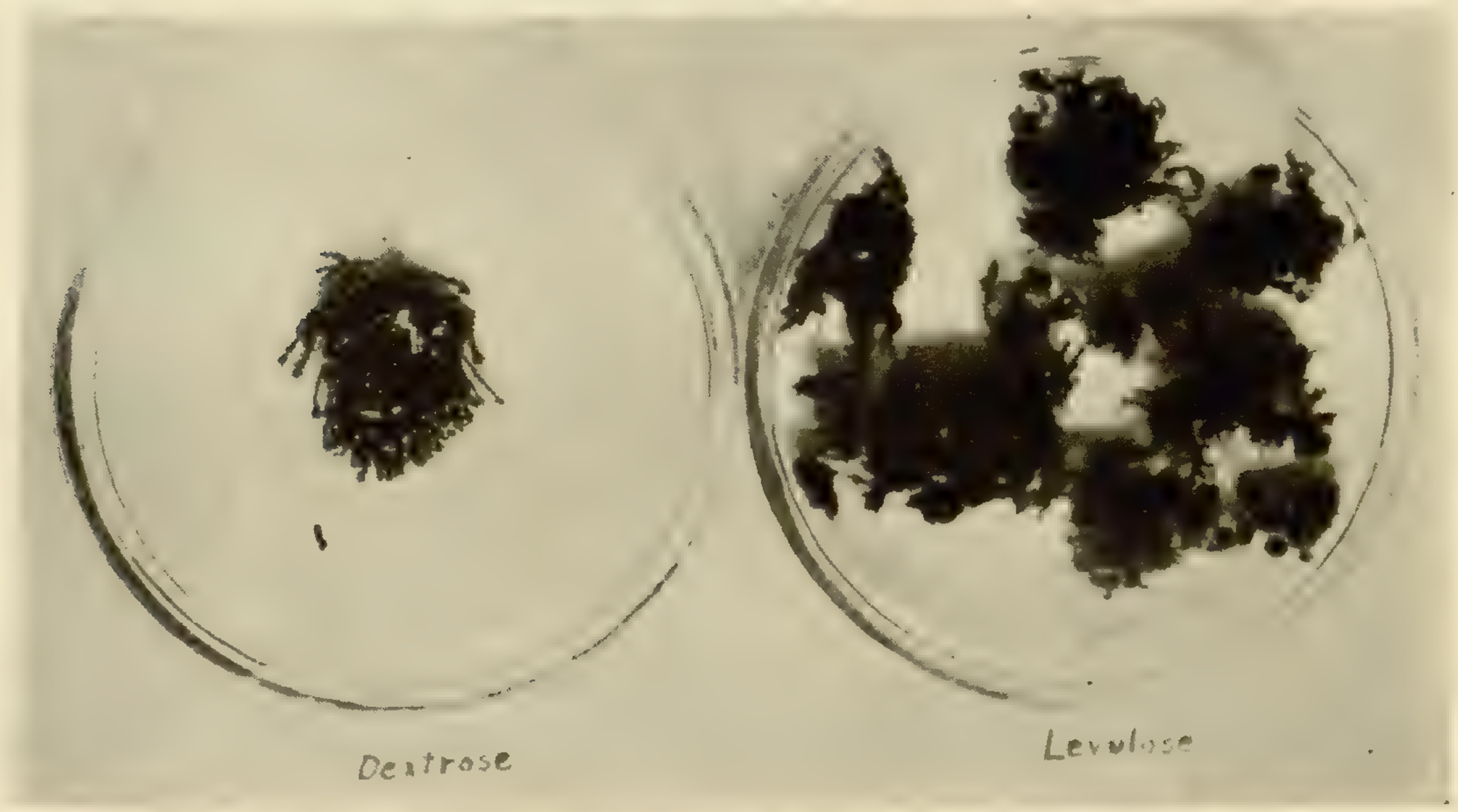

FIG. 4.—*Ceratodon purpureus* grown in nutrient solution in light for 2.5 months: on left grown in 0.1 mol. dextrose; on right in 0.1 mol. levulose.

presence of glucose in the maltose solution. No glucose was found in the lactose solution.

In the light there was growth in all the cultures, showing that none was toxic to the moss. The greatest amount of growth was found in the levulose solution. Moss plants developed in all cultures. To some extent the macroscopic appearance of the growth in the light seemed to be influenced by the particular sugar used. For example, in the glucose solution sharp clean cut moss plants were produced. In the levulose solution many moss plants were formed, but they were shorter and thicker. This difference in the moss plants and the excess of protonema in the levulose solution gave the culture as a whole a woolly appearance. The

effects of glucose, levulose, and maltose on the moss are shown in figs. 3 and 4. The cultures also differed in color. The protonema in the levulose, glucose, and cane sugar was brownish at the end of the experiment; while in the lactose, maltose, and check it was still a normal green.

COMPARISON OF LEVULOSE AND GLUCOSE AS CARBON SOURCES.—In the preceding experiment the growth when levulose was the source of carbon was so much greater in amount (fig. 5) than that when glucose was the source of carbon that a further comparison of the effects of the two sugars was made. The moss was grown from

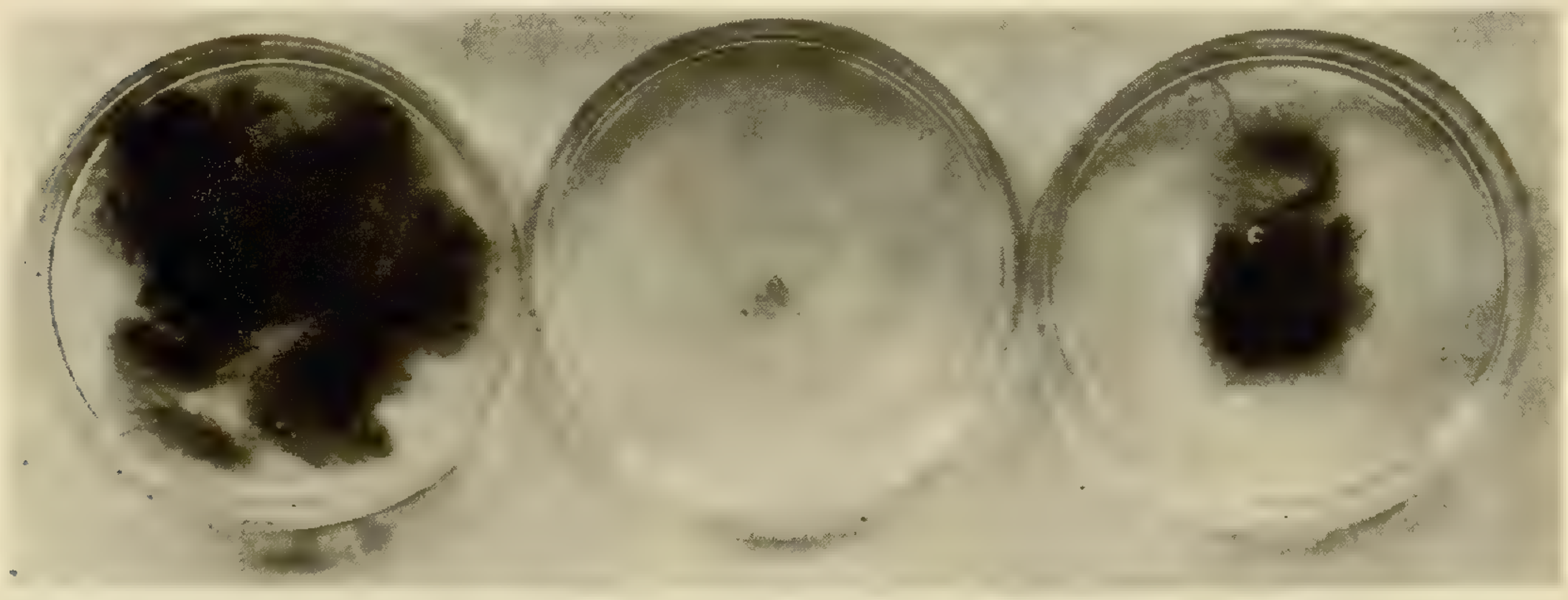

FIG. 5.—*Ceratodon purpureus* grown in dark for 2 months in nutrient solution: from left to right, 0.1 mol. levulose, no carbohydrate, 0.1 mol. glucose.

November 27 to February 24 in the modified Czapek's solution mentioned. Triplicate cultures were grown in the light and in the dark. The dry weight of the moss was determined by filtering the protonema and moss plants into a Gooch crucible and drying at 110° C. The sugar determinations were made by the use of Fehling's solution. The results are given in table II and represent the averages of the data for triplicate cultures.

The sugar analyses given in table II show an unmistakable consumption of sugar in all cases. More levulose was used than glucose. In the case of levulose the greater consumption of sugar occurred in the dark. In the case of glucose the greater consumption occurred in the light. Comparing the dry weights of the moss protonema and plants in the check, glucose, and levulose solutions, it is evident that the sugar has greatly increased the

amount of dry matter. The dry matter of the moss grown in the solution containing levulose is much greater than that of the moss grown in the solution containing glucose. In the light twice as much dry matter was formed with levulose as the carbon source than with glucose as the source of carbon. In the dark there was produced in the levulose solution 7 times as much dry matter as was formed in the glucose solution.

TABLE II

Solution	Average dry weight of moss	Original sugar per 50 cc.	Sugar used per 50 cc.	Sugar over dry weight
	gm.	gm.	gm.	
Levulose in light	0.0634	0.7700	0.1100	1.7
Levulose in dark	0.0854	0.7700	0.1650	1.9
Glucose in light	0.0345	0.8970	0.0440	1.3
Glucose in dark	0.0115	0.8970	0.0360	3.1
Check, no organic carbon in light	0.0074			
Check, no organic carbon in dark	Inappreciable			

Discussion

It is evident that the moss used in these experiments can absorb and utilize organic carbon. The experiments do not demonstrate that the mosses under field conditions, in competition with both the bacteria and the fungi, benefit from the organic compounds in the soil. They do suggest, however, that if suitable organic compounds are present in the soil solution they will be absorbed and used by the moss with advantage.

The results at present seem to bear little on the problems of the products formed in photosynthesis. It is an interesting fact, however, that starch was formed from the maltose and lactose, although no evidence was found that either of these sugars was hydrolyzed. They may have been hydrolyzed within the moss cells, or the products of hydrolysis may have been assimilated as fast as they were formed. In either of these cases evidence of the hydrolysis would have escaped the methods used in looking for it. It should also be noted that the growth in the lactose solution was very slight. An examination of the moss for the enzymes, maltase and lactase, would seem pertinent.

The differences in the growth in the levulose and glucose solutions are of considerable interest. BROWN and MORRIS (1), working with *Tropaeolum majus*, believe that glucose is more quickly used up for respiration and possibly also for tissue forming than is levulose. LINDET (4), working with the yeast and fungi, concluded that glucose is mainly concerned in respiration, while levulose is more particularly concerned in the elaboration of tissue. In the case of *Ceratodon purpureus* the elaboration of tissue is certainly far greater with levulose than with glucose. The data, although not conclusive, also suggest that the elaboration of tissue in the presence of levulose is more economical than in the presence of glucose, as the sugar used per unit of dry matter formed is generally smaller in the levulose than in the glucose solution.

Summary

1. Under the conditions of the experiments reported organic carbon in the form of levulose, glucose, galactose, lactose, cane sugar, and maltose is absorbed and utilized by *Ceratodon purpureus*.

2. Starch is formed in the dark from levulose, glucose, galactose, lactose, cane sugar, and maltose.

3. Mannite, glycerine, and starch cannot be utilized by this moss.

4. The amount of growth with levulose as the source of carbon is 2–7 times greater than that with glucose as the source of carbon.

5. In the presence of levulose the greater amount of growth occurs in the dark. With glucose the greater amount of growth occurs in the light.

6. Light seems to be necessary for the formation of moss plants, even though available carbohydrate is furnished.

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LITERATURE CITED

1. BROWN, H. T., and MORRIS, G. H., A contribution to the chemistry and physiology of foliage leaves. Jour. Chem. Soc. Trans. **63**:604–677. 1893.
2. DOX, A. W., The intracellular enzymes of *Penicillium* and *Aspergillus* with special reference to those of *Penicillium camembertii*. U.S. Dept. Agric., Bur. An. Ind. Bull. 120. pp. 70. 1910.

3. KNUDSON, L., Influence of certain carbohydrates on green plants. Cornell Univ. Agric. Exp. Sta. Mem. **9**:1–75. *figs. 11.* 1916.
4. LINDET, L., Sur le pouvoir électif des cellules végétales vis à vis du dextrose et du lévulose. Compt. Rend. **152**:775–777. 1911.
5. REED, H. S., The value of certain nutritive elements to the plant cell. Ann. Botany **21**:501–543. *figs. 2.* 1907.
6. SERVETTAZ, CAMILLE, Recherches experimentelles sur le développement et la nutrition des mousses en milieux stérilisés. Ann. Sci. Nat. Bot. IX. **17**:111–224. *pls. 4. figs. 11.* 1913.
7. VON UBISCH. G., Sterile Mooskulturen. Ber. Deutsch. Bot. Gesells. **31**:543–552. *figs. 10.* 1913.

SYSTEMATIC RELATIONSHIP OF CLITHRIS

LEO R. TEHON

(WITH PLATE IX)

The genus *Clithris* was described by FRIES (Syst. Myc. **2**:186) in 1823. Apparently unaware of this earlier description, WALLROTH (Crypt. **2**:422) erected the genus *Colpoma* in 1833, and CORDA (Icon. **5**:34) the genus *Sporomega* in 1840. FRIES'S genus was entirely overlooked and the two others accepted, so that they appear in SACCARDO'S *Sylloge Fungorum* (**2**:801; **5**:1127) in 1883 and 1891. In 1896, however, REHM (Rabenh. Krypt. Fl. **3**:101) called attention to the earlier name as follows:

> Unter obigem Namen (*Clithris* 1823), welcher die Priorität besitzt, stelle ich sowohl *Colpoma* Wallr. 1833! mit aussen bereiften Apothecien, als *Sporomega* Corda 1840! mit schwarzen Apothecien zusammen, da der innere Bau, wie die Entwicklungsweise der Apothecien bei beiden die gleichen sind.

In his subsequent treatment of the genus *Clithris*, nearly all of the species are listed which were included by SACCARDO under *Colpoma* and *Sporomega*. SACCARDO (Sylloge Fung. **18**:165) in 1906 accepts REHM'S correction and records *Colpoma* and *Sporomega* as synonyms of *Clithris*.

FRIES and KARSTEN (Mycol. Fenn. **1**:221) placed *Clithris* next to *Cenangium*, while QUÉTLET (Enchir. Fung. 330) placed *Colpoma* among the Patellariaceae. SACCARDO at first listed *Colpoma* and *Sporomega* with the Hysteriales; but later, combining the two genera under *Clithris*, he places the whole with the Phacidiales.

In the light of what has just been said, the taxonomic relationship of the genus may appear uncertain; and, indeed, when specimens are examined, the difficulty is seen to be real. Characterized by a more or less linear ascoma which opens by a longitudinal split, the superficial aspect fits very well into the concept of an Hysteriaceous form. When there is added to this the fact that in many specimens the split is small and does not expose very widely the fruiting disk, the Hysteriaceous aspect is strengthened. It is not

surprising, therefore, that the position of *Clithris* has been questioned. That these superficial characters are not sufficient for a full diagnosis of relationship becomes at once evident, and the need of an exact statement is obvious.

In making the present study, there have been available authentic specimens of *Clithris quercina* (Pers.) Rehm (Fungi Selecti Exsiccati, *Roumeguére*, no. 268, and Mycotheca Universalis, *De Thumen*, no. 369); *C. verrucosum* Wallr. (Fungi Selecti Exsiccati, *Roumeguére*, no. 2827); *C. andromedae* (Schwein) Lindau (North American Fungi, *Ellis*, no. 155); and, through the kindness of E. A. Burt of the Missouri Botanical Gardens, *C. crispa* (Pers.) Rehm (*Romell*, Fungi Exsiccati Praesertim Scandinavici, no. 85). In addition to these, use has been made of the new species described in this paper.

Material from all of these specimens has been sectioned and studied, and camera lucida drawings made of such as are not already illustrated. An examination of sectioned and unsectioned ascomata showed the following:

1. The fruiting disk is large and of densely crowded asci and paraphyses (figs. 3, 6; 8–11). This is a thoroughly Phacidiaceous character, distinct from Hysteriaceous forms, where the fruiting disk is small and seldom with asci and paraphyses overcrowded.

2. The ascigerous hymenium is characteristically Discomycetous in nature (figs. 3, 6, 8–11). The Hysteriales are regarded as forming a bridge between the Discomycetes and the Pyrenomycetes; and consequently the more disklike the hymenium the less relationship the form may be expected to bear toward the Hysteriales.

3. The opening of the ascoma is a true split (figs. 8–10). Its edges are jagged and torn; it is wider at some places than at others; and portions of the edges are frequently broken completely away in the tearing (figs. 2, 11). Opposed to this character is the rather regular appearance of the edges of the openings in Hysteriaceous forms which suggests that the slit there is an elongated ostiole rather than a true split or tear.

4. The tendency in the specimens examined is to find the fruiting disk in places rather widely exposed, either by the wide bending back of the sides of the ascoma (figs. 3, 10) or by the

breaking off of portions of the top (figs. 6, 11). Hysteriaceous forms have the fruiting disk nearly or quite covered.

Strengthening these observations are the conditions to be observed in the new species of *Clithris* herewith described. *C. clusiae* (figs. 2, 3) shows the characteristically Discomycetous hymenium, and the tendency to expose the fruiting disk by the breaking off of portions of the roof of the ascoma. In the section it will be seen that the top has broken away completely, thus leaving the entire fruiting disk exposed. Almost the same conditions are to be found in *C. minor*. *C. pandani* (fig. 6) likewise shows the characteristically Discomycetous hymenium. Of the top of the ascoma there remain only small projections on either side. The center has broken away, leaving a very large part of the fruiting disk exposed.

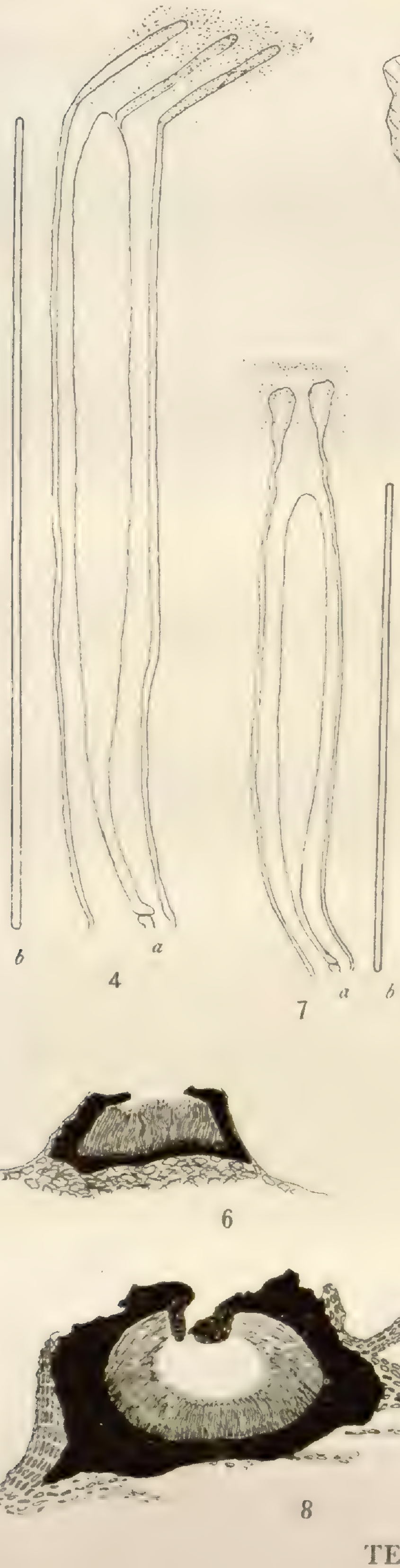
CLITHRIS Fries, 1823.—As originally described, *Clithris* is characterized in part by the possession of paraphyses coiled at the tip. Obviously, the form of the tips of the paraphyses cannot be held as a generic character, since the three species here described, which are clearly congeneric, show certain variations as regards the paraphyses tips, one only possessing the characteristic coiling. These species were collected by F. L. STEVENS in Porto Rico, and it is through his kindness that the author is allowed to include descriptions of them in this paper.

Clithris clusiae, sp. nov.—Spots 0.5–2 cm. in diameter, pale to yellow, uniformly dotted with the ascomata. Ascomata dark, subepidermal, erumpent, 950×468 μ, rupturing with the epidermis in a long slit. Paraphyses filiform, numerous, coalescing above in a pale yellow epithecium. Asci long, narrow, 150×7–8 μ, 8-spored; spores filiform, 1×150 μ, fragmenting when mature, pale smoky or light brown.

On dead leaves of *Clusia rosea*. Desecheo Island no. 1595 (type).

The ascomata of this species are to be found not only in spots on the leaf blade but also clustered very thickly on the petiole and the midrib. The paraphyses are not coiled apically, but slightly enlarged and straight. The tip bends just above the top of the asci, as is shown in fig. 4*a*.

Clithris minor, sp. nov.—Spots similar to those of *C. clusiae*. Ascomata small, dark, 624×220 μ. Paraphyses numerous, filiform,



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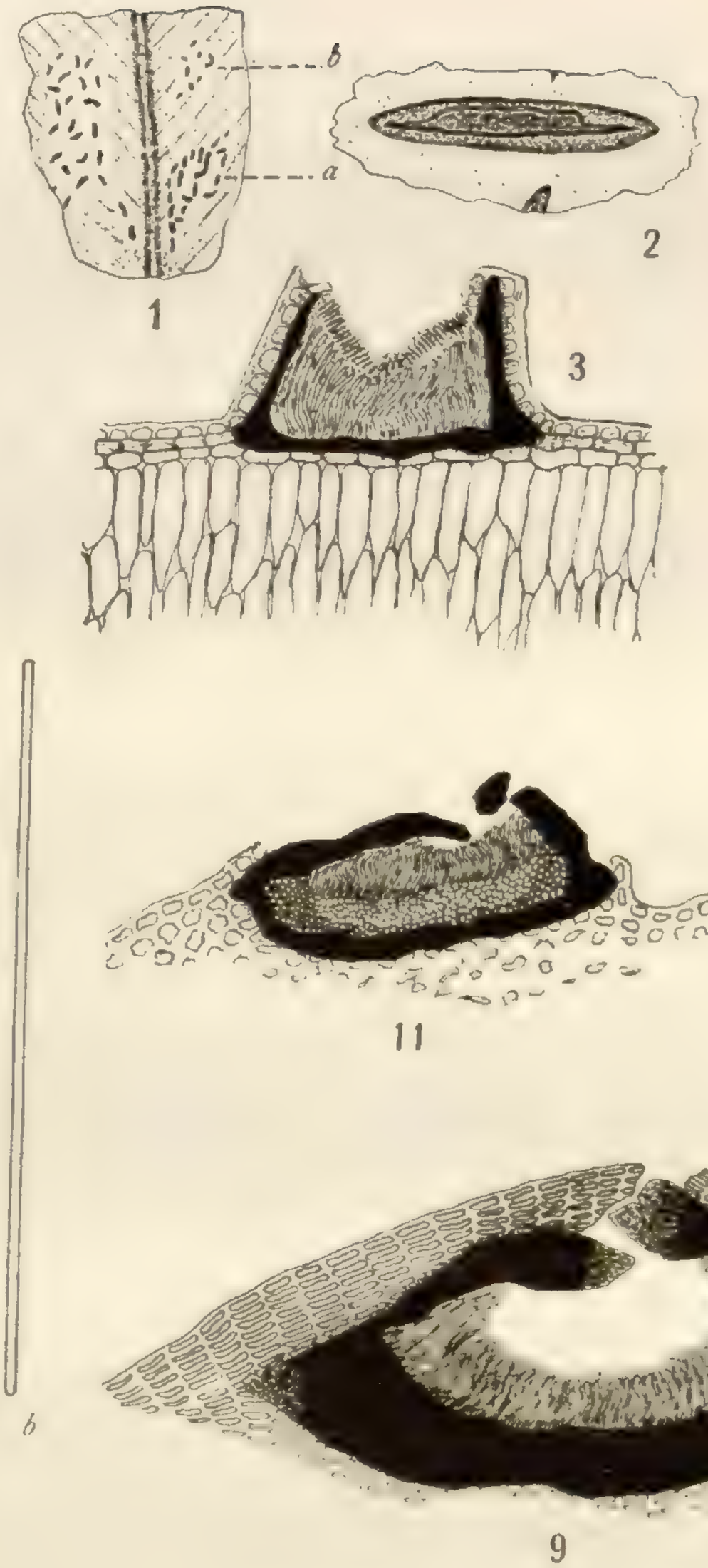

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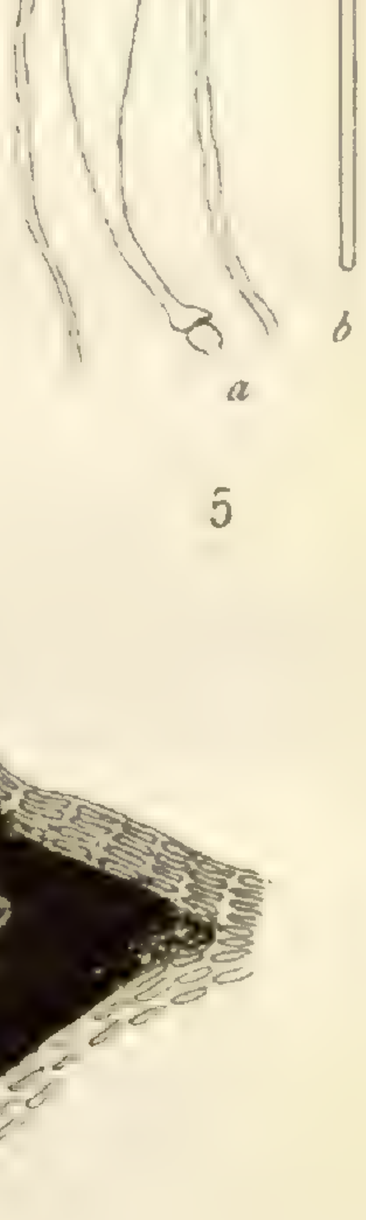

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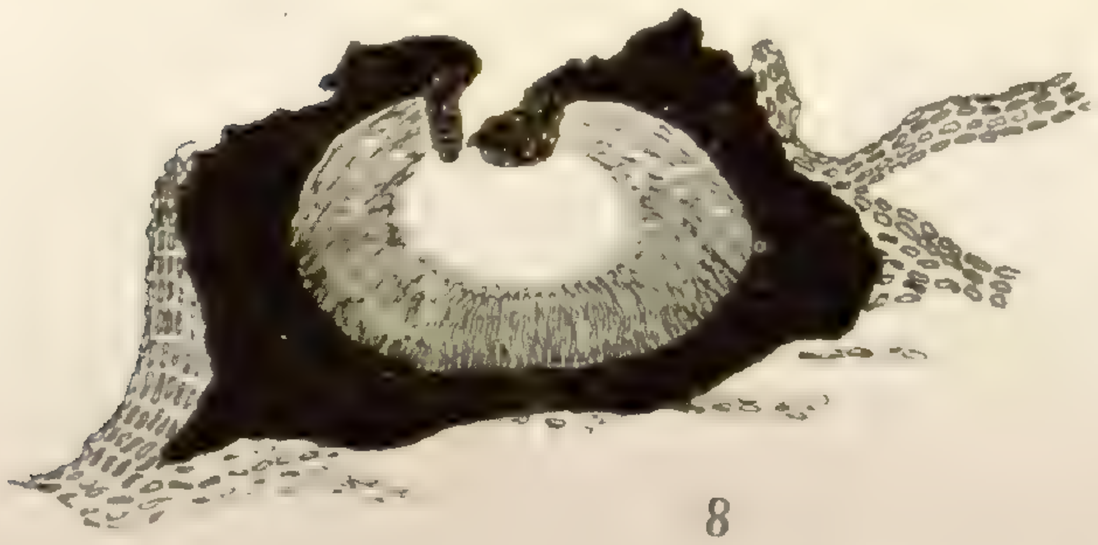

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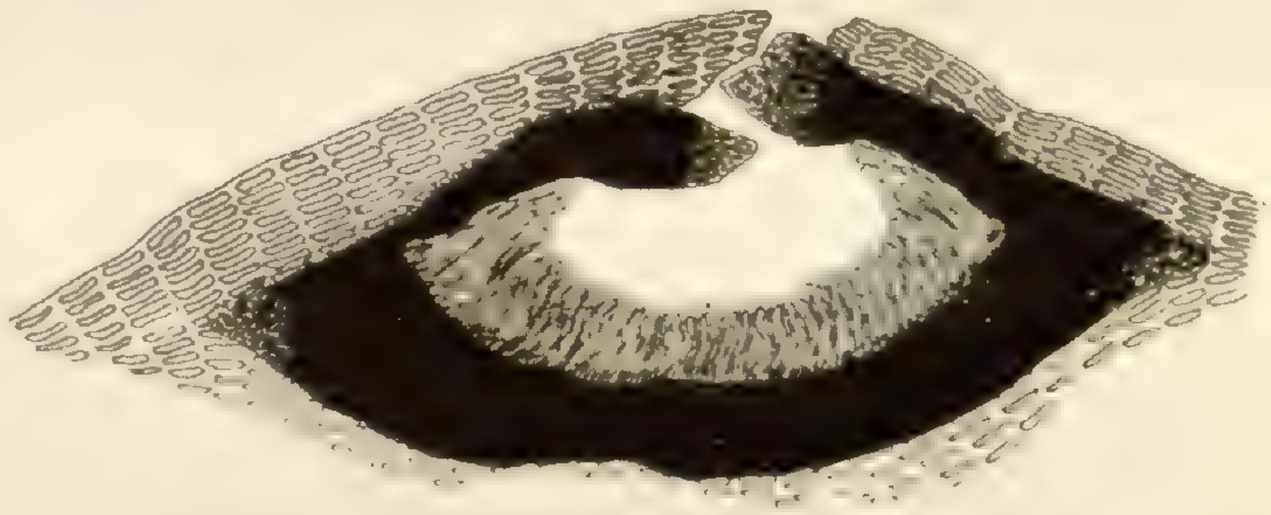

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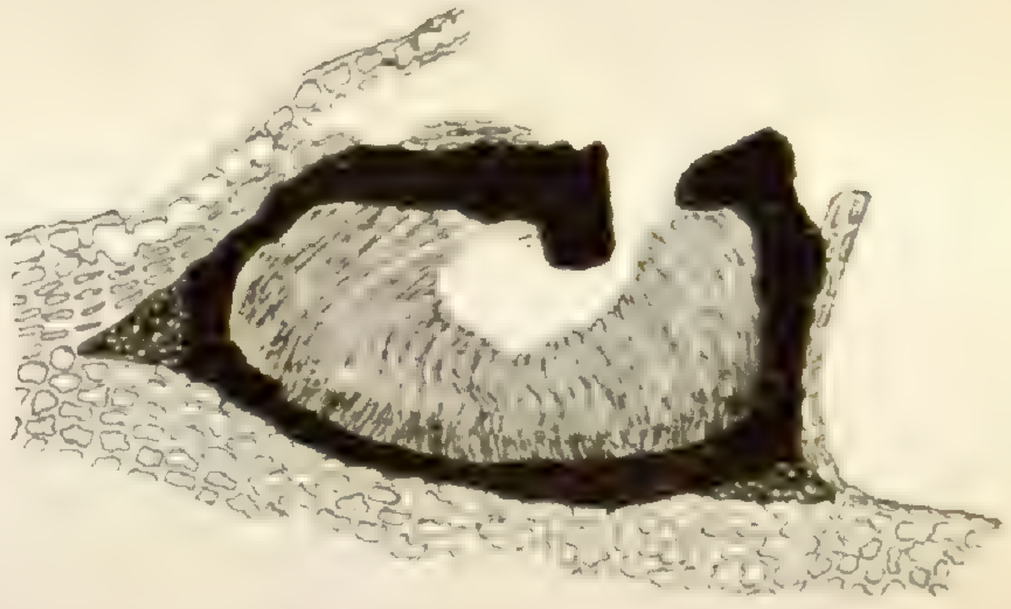

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TEHON on CLITHRIS

hyaline, slightly exceeding the asci and coiled apically to form a thin, hyaline epithecium. Asci long, narrow, 110×7 μ, 8-spored; spores filiform, 1×110 μ, fragmenting when mature, and pale smoky in color.

On dead leaves of *Clusia rosea*. Desecheo Island, no. 1595 (type).

Although occurring on the same leaf with *C. clusiae*, *C. minor* is readily distinguished by its smaller size, and by the abundance of hyaline paraphyses which only slightly exceed the asci and are coiled apically, forming a thin, hyaline epithecium.

Clithris pandani, sp. nov.—Spots 0.25–1 cm. in diameter, otherwise similar to those of *C. clusiae* and *C. minor*. Ascomata small, dark, subepidermal, erumpent, 570×110 μ. Paraphyses numerous, exceeding the asci and united above into a pale yellowish epithecium. Asci long, narrow, 91×7 μ, 8-spored; spores filiform, 1×91 μ, fragmenting when mature, and pale smoky in color.

On dead leaves of a cultivated species of *Pandanus*. San Juan, no. 4090 (type).

This species is the smallest of the three; otherwise its superficial characteristics are much like those of *C. clusiae* and *C. minor*. The tips of the paraphyses are expanded above (but not coiled) and united into a pale yellowish epithecium.

Types of these species are deposited in the Herbarium of the University of Illinois.

UNIVERSITY OF ILLINOIS

EXPLANATION OF PLATE IX

FIG. 1.—Habitat sketch: *a*, *C. clusiae*; *b*, *C. minor*.
FIG. 2.—Habitat sketch of *C. clusiae*, enlarged.
FIG. 3.—*C. clusiae:* section of ascoma.
FIG. 4.—*C. clusiae:* *a*, asci and paraphyses; *b*, spore.
FIG. 5.—*C. minor:* *a*, asci and paraphyses; *b*, spore.
FIG. 6.—*C. pandani:* section of ascoma.
FIG. 7.—*C. pandani:* *a*, asci and paraphyses; *b*, spores.
FIG. 8.—*C. crispa:* section of ascoma.
FIG. 9.—*C. andromedae:* section of ascoma.
FIG. 10.—*C. quercina:* section of ascoma.
FIG. 11.—*C. verrucosum:* section of ascoma.

STRUCTURE OF WOOD IN BLUEBERRY AND HUCKLEBERRY[1]

ESTHER MARGARET FLINT

(WITH PLATES X, XI)

According to EAMES,[2] the anatomy of the northern oaks is characterized by small uniseriate rays, and large ones which are many cells in width and generally fusiform in shape. It has been shown in this article that the large rays have developed from the aggregation of small ones through the transformation of fibers into parenchyma. As evidence he figures the wood of *Quercus*, especially seedlings, to elucidate the broad ray in the process of formation by fusion of small rays, and the gradual transformation of the separating fibers into parenchymatous elements. A study of the material investigated by EAMES justifies his conclusion. As a preliminary to the present investigation, some illustrations of the anatomy of a seedling oak have been introduced. Fig. 1 shows in tangential view a portion of the wood of the epicotyl of *Quercus velutina* with two characteristic kinds of rays. The broad ray in the central part is plainly in the process of formation, the parenchyma cells being interspersed with fibers in all stages of division and transformation into parenchyma. Fig. 2 is a transverse view of the situation in fig. 1. The broad ray here shows two kinds of cells, the dark parenchymatous ones, and the lighter ones which represent more or less modified fibers. Fig. 3 shows a view in the same plane as fig. 1, but more highly magnified. The manner in which the ray becomes solidly parenchymatous is even more apparent here, especially at the left of the figure, where we see a fiber partially divided into parenchyma cells.

With this preliminary reference to the anatomy of *Quercus*, it is possible to pass advantageously to the consideration of the anatomy of *Vaccinium* and allied genera, which show interesting and strik-

[1] Contribution from the Laboratory of Plant Morphology of Harvard University.

[2] EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. **49**: 161–167. *pls. 8, 9.* 1910.

ing points of similarity with the conditions already mentioned. *V. corymbosum*, as shown in transverse view by fig. 4, is seen to have broad and also uniseriate rays, as does *Quercus*. Although the large rays are not so broad as the corresponding rays of the oak, yet they are similar to the latter in the strong contrast which they present to the small uniseriate ones. The large ray of *V. corymbosum* (fig. 4) is composed of two kinds of cells: light, rather larger ones; and dark, smaller ones (the ordinary parenchymatous ray cells), a condition which exactly parallels the organization of the ray of the oak just noted. Fig. 5 shows a portion of this same transverse view of the wood of the stem of *V. corymbosum* more highly magnified, so that the twofold composition of the ray becomes even more apparent. Fig. 6 is a tangential aspect of the wood of the stem of *V. corymbosum* corresponding to fig. 4. In this plane also the two kinds of rays, uniseriate and broad, are likewise visible. The presence of two kinds of cells in the large ray, one dark and rather small, the other light and somewhat larger, can also be distinguished clearly. Obviously the large ray is a compound structure, just as has been proved in the case of the corresponding large rays of the oak, with which the large ray of *V. corymbosum* appears to be identical in so far as it is composed of the two kinds of cells described.

Vaccinium pennsylvanicum shows the same situation as *V. corymbosum*, as is vouched for by figs. 7 and 8. In fig. 7 the contrast between broad and narrow rays is readily distinguished. The large number of light colored cells present in the broad ray plainly shows indication of origin from the transformation of fibrous elements into parenchyma. An enlarged view of this situation is given in fig. 8, which represents a higher magnification. The light cells are strikingly different from the ordinary ray cells which they accompany, and the seriate ones in the central portion are obviously derived from a transformed fiber. The whole structure is consequently a compound ray resembling that found in the wood of the oak. In fig. 9 the same condition is noted as in fig. 7, namely, rays of two sharply contrasting types, broad and uniseriate. Of these the large ones are compound in structure, showing derivation by the fusion of small rays as well as by the transformation

of fibers into parenchyma cells. This figure represents in tangential view the wood of the root of *Gaylussacia*, a genus closely allied to *Vaccinium* and having identical ray structure, as is seen by the comparison of the two woods illustrated in figs. 7 and 9.

Fig. 10 is a tangential view of the wood of the root of *Rhododendron*, a genus also allied to *Vaccinium* although not so closely as is *Gaylussacia*. The wood as shown here is much like that of the northern oaks, especially in the marked contrast between its large and small rays. The construction of the ray itself in *Rhododendron*, however, is more clearly seen in fig. 11, a transverse section of the same wood. The interspersion of the light colored fibrous elements through the ray at once shows its composite character, and although it does not illustrate actual transformation of fibers into radial parenchyma, it points the way to that as a natural solution of the origin of the broad ray in this genus.

In regard to *Vaccinium* and the allied *Gaylussacia* it is now clear that the large rays in these genera are of the same nature as those of *Quercus*, and like them are in strong contrast to the more numerous uniseriate rays. In *Rhododendron* also we noted the same condition, albeit its origin was not in all respects so clear. That this condition of *Vaccinium* and allied genera, which is so similar to that found in the oak, is not common to all ericaceous woody types, is evidenced by fig. 12, which shows in tangential view the wood of the stem of a species of *Arbutus*. The rays of this wood do not fall into two strongly contrasting categories, the broad and the uniseriate. Rather do they grade into each other and are only relatively broad or narrow when compared with each other. In this respect *Arbutus* presents the general situation for forest trees, the majority of which do not possess contrasted broad rays and uniseriate rays, but have all their rays comparatively small and of intergrading dimensions.

From this examination of the genus *Vaccinium* and other genera allied to it, and the comparison of them with the wood of *Quercus*, we must conclude that the well known large rays of the latter have their counterparts in the somewhat smaller rays of *Vaccinium* and *Gaylussacia*. These rays, although of considerably smaller dimensions, are in just as marked contrast to the accompanying

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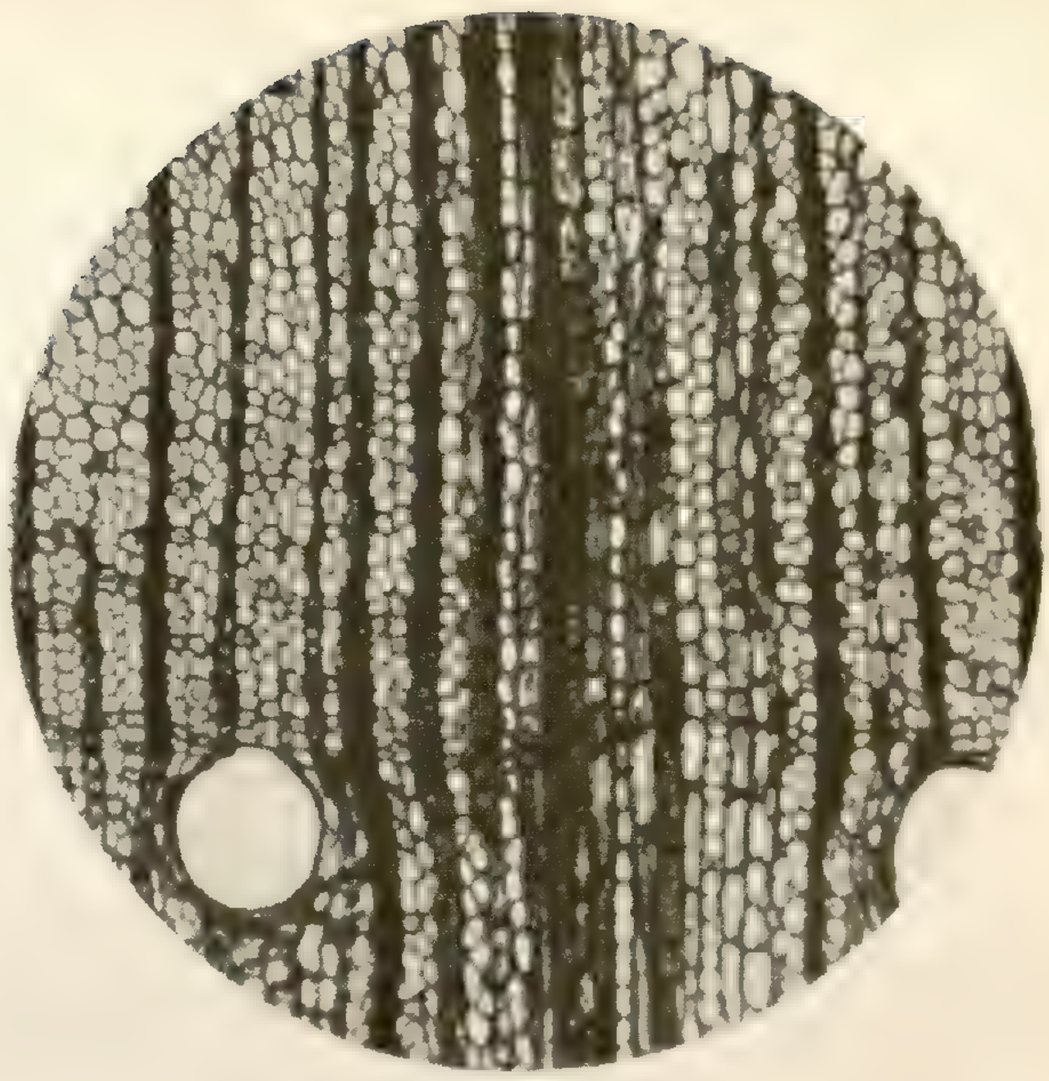

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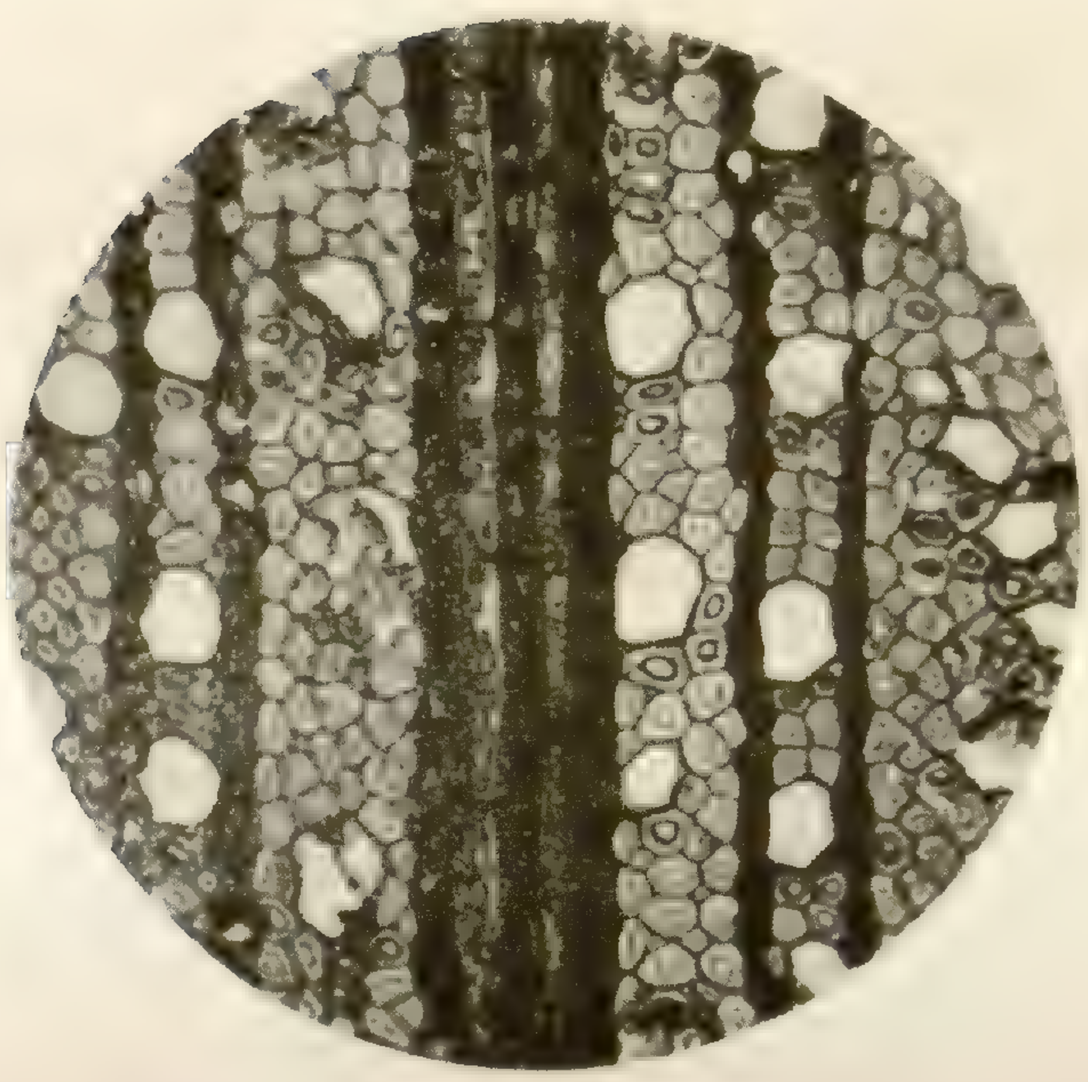

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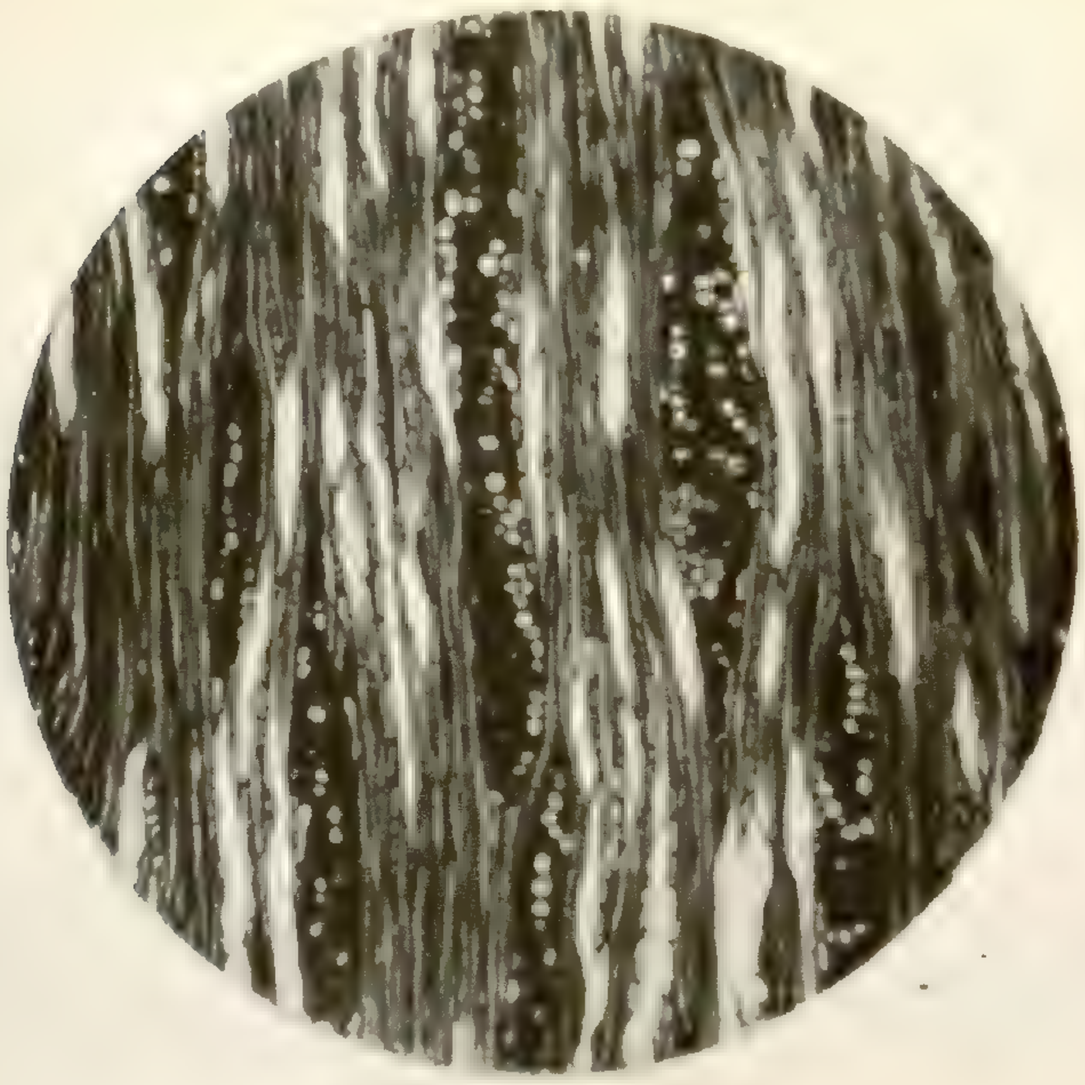
FLINT on VACCINIUM



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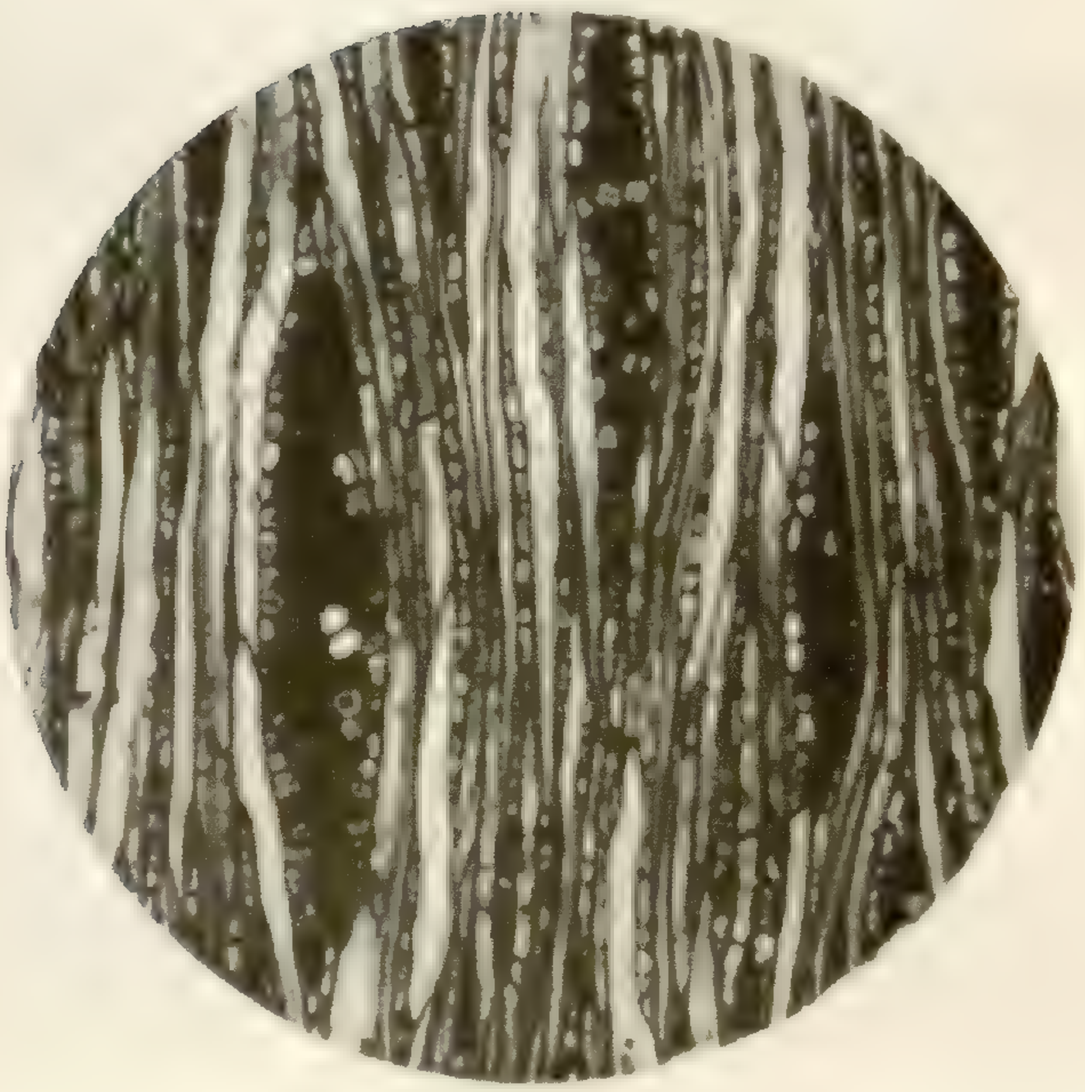

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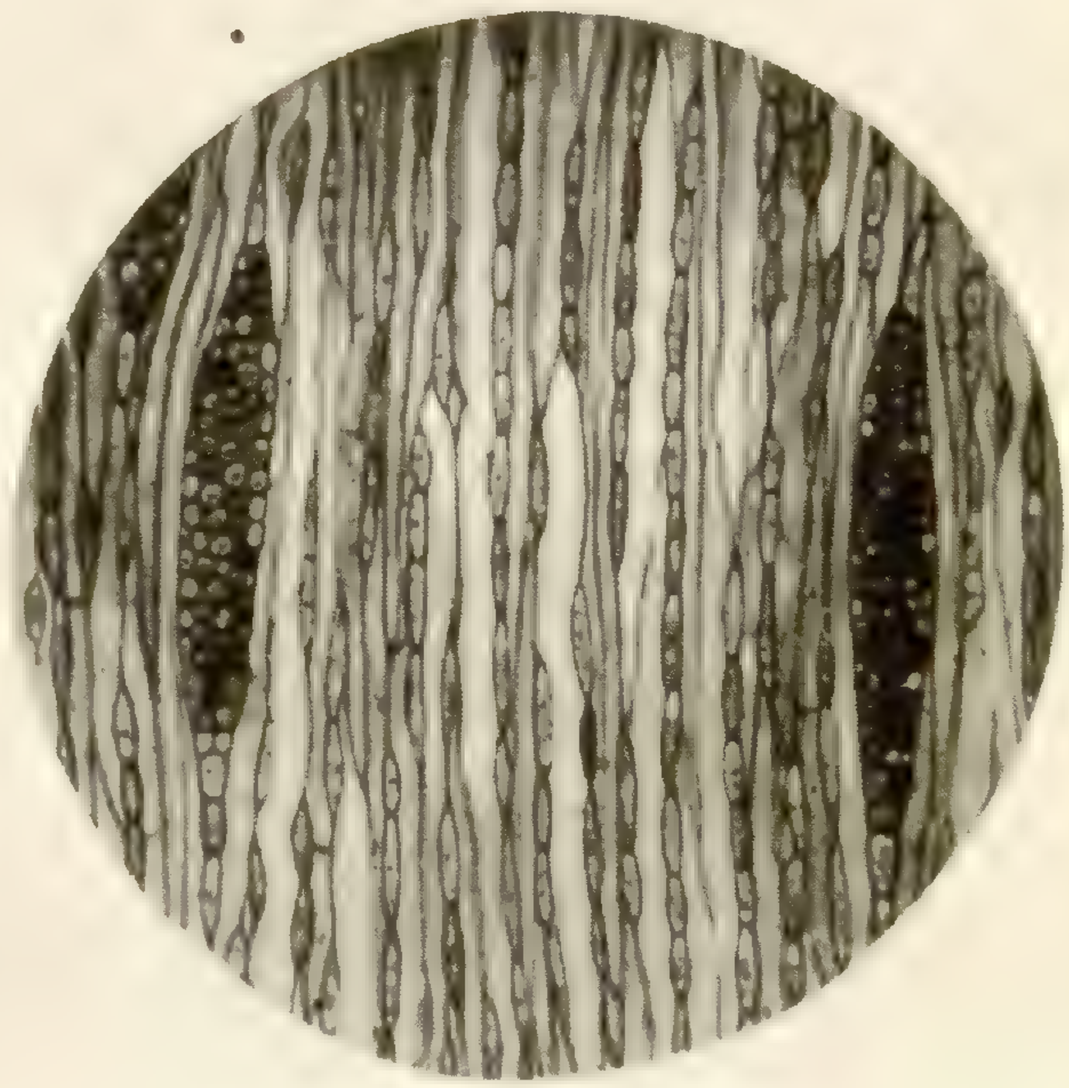

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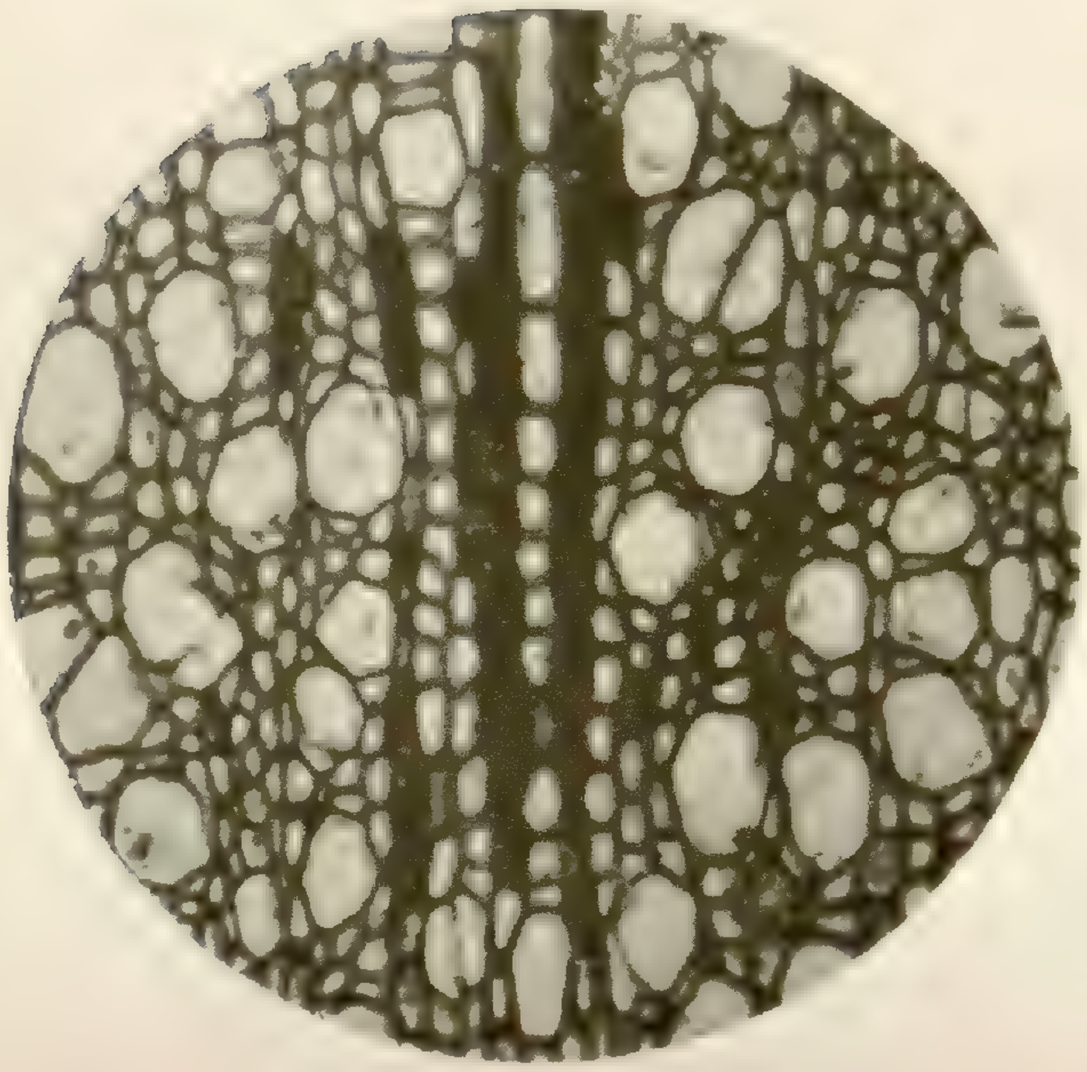

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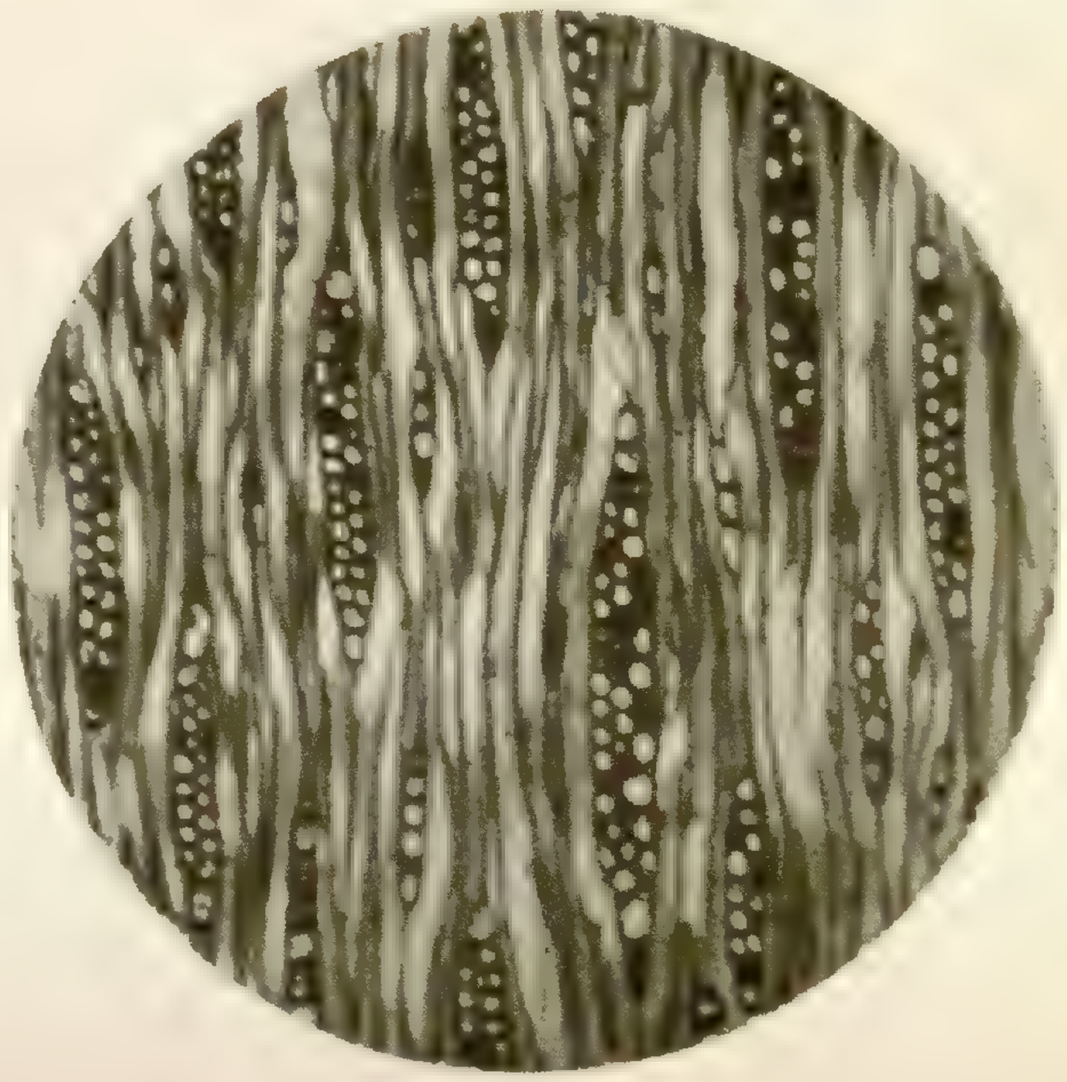

12

FLINT on VACCINIUM

uniseriate rays as are the broad rays in *Quercus*. Because of this sharp contrast, and because of the similar origin of the broad rays, they are obviously the exact counterparts of the broad parenchymatous bands in the secondary wood of *Quercus*.

In conclusion, I wish to thank Dr. E. C. JEFFREY of this laboratory for material and advice rendered during the course of this investigation.

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EXPLANATION OF PLATES X, XI

FIG. 1.—Longitudinal tangential section, aggregate ray of seedling of *Quercus velutina;* ×100.

FIG. 2.—Transverse section, wood of seedling of *Q. velutina;* ×100.

FIG. 3.—Longitudinal tangential section, wood of *Q. velutina;* ×200.

FIG. 4.—Transverse section, wood of stem of *Vaccinium corymbosum;* ×100.

FIG. 5.—Transverse section, wood of stem of *V. corymbosum;* ×200.

FIG. 6.—Longitudinal tangential section, wood of stem of *V. corymbosum;* ×100.

FIG. 7.—Longitudinal tangential section, wood of subterranean stem of *V. pennsylvanicum;* ×100.

FIG. 8.—Longitudinal tangential section, wood of root of *V. pennsylvanicum;* ×200.

FIG. 9.—Longitudinal tangential section, wood of root of *Gaylussacia* species; ×100.

FIG. 10.—Longitudinal tangential section, wood of root of *Rhododendron* species; ×100.

FIG. 11.—Transverse section, wood of root of *Rhododendron* species; ×200.

FIG. 12.—Longitudinal tangential section, wood of stem of *Arbutus* species; ×100.

BRIEFER ARTICLES

PURPLE BUD SPORT ON PALE FLOWERED LILAC (SYRINGA PERSICA)

(WITH ONE FIGURE)

In the present state of our knowledge of bud sports, every well authenticated case is distinctly worthy of record. Fig. 1 represents a panicle of a bud sport of the Persian lilac, and beside it a panicle of the form on which it appeared. The bush is one of the very pale-flowered varieties, by no means white, which is best described as lilac-tinged. The bud sport was deep purple, of exactly the same color as the darkest flowered variety of the Persian lilac commonly grown. The sport was free from all suspicion of being a graft, occurring, as it did, at the summit of a bush 10 ft. high, which had never been grafted, with normal panicles of the same age below it. The bush has flowered for 10 years or more, without ever having produced any other than tinged flowers. Dr. LOUIS P. HALL, of Ann Arbor, on whose grounds it occurred, and who called it to our attention, is a keen observer, and would surely have noticed unusual panicles if there had been any before this year. Particular pains were taken to ascertain that the sport was truly such, and not a graft, for grafted lilacs are, of course, not uncommon. The evidence that the dark-colored inflorescence was the result of a bud sport was altogether clear.

The flowers of the variation differed from those of the form on which it occurred not only in color but also in size. Data for several size characters, based in each case upon 50 measurements, are as follows:

	Normal form	Purple bud sport
Spread of corolla		
Range	10.4–13.3 mm.	15.3–18.4 mm.
Mean	12.2	16.6
Length of tube		
Range	9.9–11.9	10.2–11.8
Mean	11.3	11.1
Width of corolla lobes		
Range	2.7–4.1	4.0–5.5
Mean	3.6	4.75

It is evident that the chief size differences are in the spread of the corolla and the width of its lobes. The ranges of variation for these characters hardly overlap in the two forms.

FIG. 1.—*Syringa persica:* at left, large-flowered purple bud sport; at right, normal inflorescence of small-flowered, lilac-tinged variety.

In both measurements and color, the bud sport exactly duplicated a dark purple variety of *Syringa persica* which is commonly cultivated. The latter differs from the lilac-tinged variety in that the corolla lobes appear to be 3-nerved rather than 1-nerved. In this character, also, the bud sport was different from the bush that produced it, and exactly

like the purple variety. Microscopic examination showed that what appeared to be lateral nerves were not due to bundles, but were merely folds. Nevertheless they afford a striking character difference between the two forms.

The bushes under consideration are identified as *Syringa persica* with some doubt. The upper surface of the leaves lacks stomata, which should be present in *S. persica*, as defined by SCHNEIDER in his *Handbuch der Laubholzkunde*. The flowers are sterile, a fact which would presumably point to a hybrid ancestry, and the terminal bud is not suppressed, but generally gives rise to a panicle. The flowers are produced, then, from lateral and terminal buds on the wood of the preceding year. The bushes were purchased as *S. persica*, which seems, on the whole, the most applicable name.

The color of the wild lilacs is purple. A light-colored variety, such as the one which produced this bud sport, might be judged, a priori, to be a Mendelian recessive. If it should be found to be so, the reversion to the original purple would be distinctly interesting, from the standpoint of the now almost discarded presence and absence hypothesis. If not a reversion, it might be either a case of what has been called somatic segregation, or a periclinal chimaera. These hypotheses will be tested, if possible; but since the evidence, if obtainable at all, must be long delayed, it is thought worth while to report the mere fact that such a bud sport has been observed.—FRIEDA COBB AND H. H. BARTLETT, *University of Michigan, Ann Arbor, Mich.*

METHOD FOR STAINING ANTHEROZOID OF FERN

(WITH ONE FIGURE)

Some time ago the writer had a favorable opportunity to study spermatogenesis in some of the common ferns, and it was found desirable to perfect a staining technique by means of which it was possible to stain the cilia and at the same time to differentiate clearly the different parts of the body of the antherozoid. Of the various methods employed the following proved most satisfactory: (1) kill antherozoids in a drop of water on a slide by inverting the slide over a vial containing a 1 per cent osmic acid solution (the drop of water should be small and when placed on the slide spread out so as to form a thin film); (2) dry slide in air; (3) stain in safranin 10 minutes to 1 hour; (4) wash in water; (5) wash in 95 per cent alcohol until only the nucleus remains stained; if necessary,

use xylol to clear and then remove the xylol with 95 per cent and absolute alcohol; (6) stain in acid fuchsin 10–20 seconds; (7) wash in absolute alcohol; (8) clear in clove oil and xylol; (9) seal in balsam.

The nucleus is stained a bright red by the safranin, while the cytoplasmic portions of the antherozoid are stained a bluish pink. The blepharoplast is more densely stained than the cytoplasmic envelope.

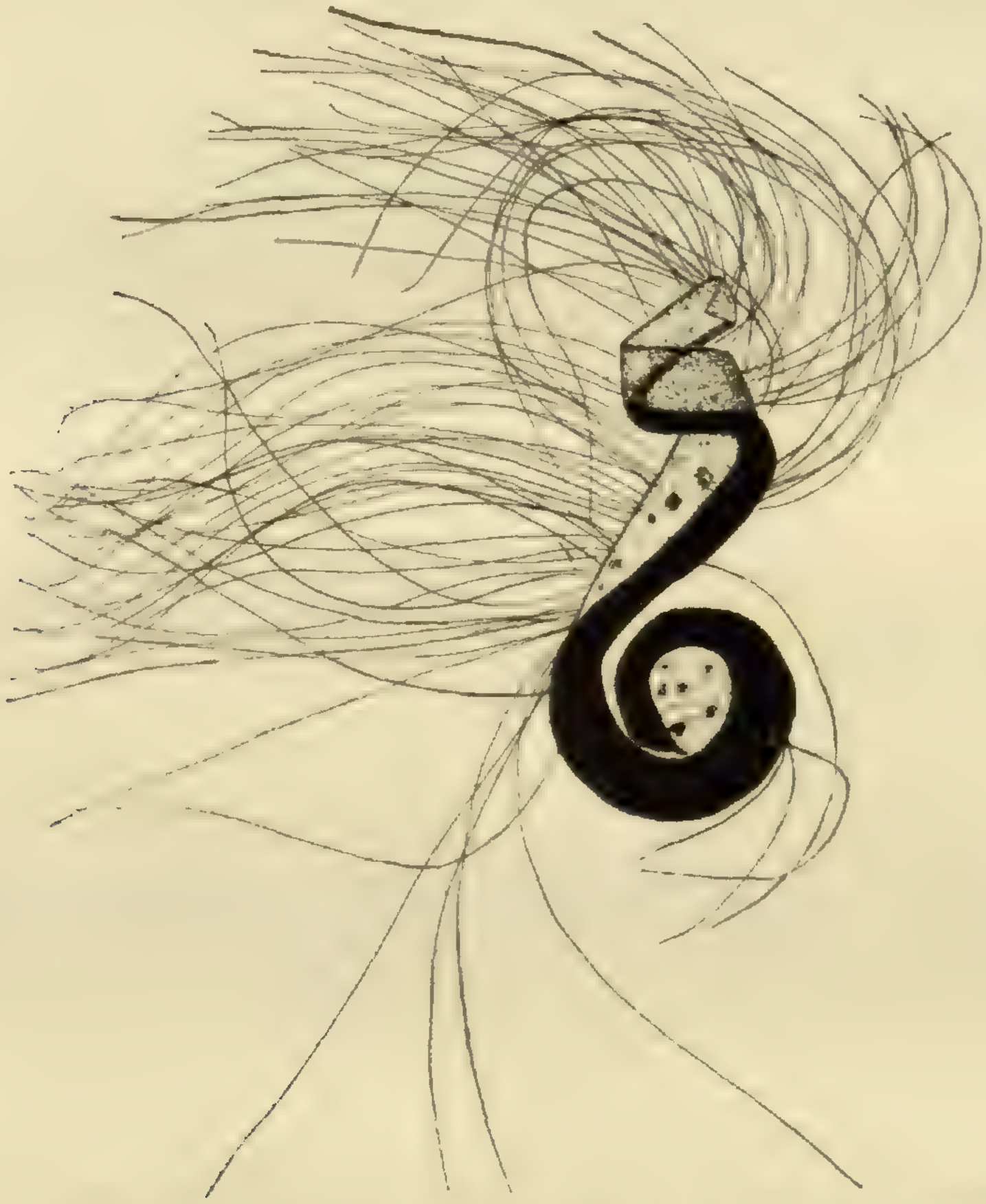

FIG. 1.—Antherozoid of *Onoclea struthiopteris*; ×3700 and reduced one-half in reproduction.

The cilia of the antherozoid are attached for some length along the blepharoplast, as shown in fig. 1. No cilia are attached to the extreme anterior portion of the blepharoplast. The envelope at the anterior end extends a short distance beyond the nucleus, which is small and rodlike at this extremity. The nature of the denser portions in the envelope is not understood. These were of constant occurrence when the method described was used. They could also be readily observed in the living antherozoid. Some very good results were obtained when iron haematoxylin was substituted for the safranin.—W. N. STEIL, *University of Wisconsin, Madison, Wis.*

CURRENT LITERATURE

BOOK REVIEWS

Botany of crop plants

A notable impetus to the study of botany in agricultural colleges and to the study of agricultural plants and problems in botanical departments generally is bound to be given by ROBBINS' recent volume on the botany of crop plants.[1] About 70 pages are devoted to a brief summation of some of the more important topics in general botany, under the headings: the seed plant body, fundamental internal structures, roots, stems, leaves, flowers, fruits, seeds and seedlings, and the classification and naming of plants. The body of the book presents in compact and pleasing form the botanical features of our chief crop plants, arranged in the familiar taxonomic sequence from grasses to composites. For each crop there is a discussion of the chief botanical features relating to habit, structure, and behavior, a classification (often with a key), a consideration of the chief uses, and a list of the more important references. As a sample of the mode of treatment we may take corn, to which 35 pages are devoted. The paragraph headings under corn are habit of plant and roots, prop roots, stem, leaves, inflorescence, staminate inflorescence, staminate spikelet, pistillate inflorescence, pistillate spikelet, hermaphroditic flowers, opening of the flowers and pollination, fertilization and development of the grain, xenia, variation, results of self-fertilization, the mature grain, corn starch, germination, classification, origin, environmental relations, uses, production, and references.

The compactness and up-to-dateness of the information in this book are among its most commendable features. It is doubtful if there is any other place where one may find so quickly and satisfactorily botanical information about our common crops. While the volume was written primarily as a text-book for botanical courses in agricultural colleges, a field which was far from adequately filled, this book should be on the shelf of every botanical teacher and investigator, because of its value as a source of ready and reliable information. The publishers also may be commended for the neat and pleasing appearance which the book presents.—H. C. COWLES.

MINOR NOTICES

Flora of Bermuda.—BRITTON[2] has published an illustrated *Flora of Bermuda* which is attractive in appearance and unusually inclusive in its contents. The land area is a little over 19 square miles, or about one-fourth the size of

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[1] ROBBINS, W. W., The botany of crop plants. pp. xix+681. *figs. 263.* Blakiston's Son & Co. Philadelphia. 1917.

[2] BRITTON, NATHANIEL LORD, Flora of Bermuda. 8vo. xi+585. *figs. 519.* New York: Scribner's Sons. 1918. $4.50.

Staten Island, but the flora calls for a book of nearly 600 pages. About 80 per cent of the land plants occur also in the West Indies or southern Florida or both, while about 8.7 per cent of the total native flora is endemic, "there being 61 species in Bermuda or its waters not known to grow naturally anywhere else in the world." The representation of groups by the native species is as follows: Spermatophytes 146, Pteridophytes 19, Bryophytes 51, Lichens 80, Fungi 175 (at least), Algae 238, making a total of 709 species. The volume contains descriptions and illustrations of 519 species of Spermatophytes, Pteridophytes, and Bryophytes, and also accounts, not illustrated, of the Lichens, Fungi, and Algae.

The excellent text cuts, simple keys, and clear descriptions should make the volume a very effective introduction to an interesting flora.—J. M. C.

NOTES FOR STUDENTS

Prothallia and sporelings of lycopods.—Recent investigations have added greatly to our knowledge of some difficult prothallia and sporelings of lycopods and, with researches now well advanced, may make these phases of the life history as clear as in the common ferns. The Lycopodiales and Psilotales will be considered separately.

LYCOPODIALES.—Among the investigators who have studied the prothallia of *Lycopodium*, two have been preeminent both in field and laboratory work, namely, TREUB, who devoted his attention to the tropical species of Java, and BRUCHMANN, who studied species of the northern temperate zone. A third investigator of the first rank must now be added, the Rev. J. E. HOLLOWAY, who has discovered and studied the prothallia and sporelings of various New Zealand species of *Lycopodium*, so that species of the southern temperate zone are now represented. Three papers[3] have already appeared and the investigation is still in progress.

The introductory paper deals with *L. volubile*, *L. scariosum*, *L. densum*, *L. laterale*, *L. cernuum*, and *L. Billardieri*, all of which, except *L. cernuum*, are confined to the islands and countries of the south Pacific. He found prothallia of all except *L. densum*, so that 4 species are recorded for the first time, *L. cernuum* having been described by TREUB. Only a brief mention is made of the prothallia, the paper dealing, as its title indicates, with the comparative anatomy. The structure of the stele in young and adult plants is compared, and it is clearly shown that the radial type is primitive and that the banded type is derived from it.

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[3] HOLLOWAY, J. E., A comparative study of the anatomy of six New Zealand species of *Lycopodium*. Trans. New Zealand Inst. **42**:356–370. *pls. 31–34*. 1909.

———, Studies in the New Zealand species of the genus *Lycopodium*. Part I. Trans. New Zealand Inst. **48**:253–303. *pls. 17, 18. figs. 102*. 1916.

———, Studies in the New Zealand species of the genus *Lycopodium*. Part II. Methods of vegetative reproduction. Trans. New Zealand Inst. **49**:80–93. *pls. 8, 9. figs. 24*. 1917.

The second paper deals with 11 species, including the 6 already mentioned, and adding *L. varium*, *L. Drummondii*, *L. fastigiatum*, *L. ramulosum*, and *L. Selago*. Since all these species, with the exception of *L. cernuum* and *L. Selago*, are rather unfamiliar to European and American botanists, the writer describes the habit, habitat, and environmental conditions. The ecological treatment, based upon an immense amount of field work, is particularly interesting, since some of the species are epiphytic and some terrestrial, and, of the latter, some belong to wet and some to dry habitats. Young plants and prothallia are not found in localities where adult plants are abundant, but in places like roadside cuttings where the soil has been disturbed. It is estimated that 15 years may elapse from the germination of the spore of *L. fastigiatum* to the fully developed prothallium; while species like *L. cernuum*, *L. ramulosum*, and *L. laterale* develop their more or less aerial and green prothallia in a single season.

Since the 11 species described by TREUB, BRUCHMANN, and others showed 5 distinct types of prothallia, it is surprising to find that among the various prothallia discovered by HOLLOWAY, no strictly new type has appeared. There are interesting variations, but the divergences are not sufficient to warrant an additional category. He believes that the *Lycopodium* prothallium is in a plastic stage of evolution, and that the various types have not been genetically distinct from a very remote period, but have diverged from the *L. cernuum* type, which now includes *L. inundatum*, *L. salakense*, *L. laterale*, and *L. ramulosum*, and is the only one which has shown a protocorm stage in the embryogeny. In *L. laterale* and *L. ramulosum* a protocorm grows out into a rhizome-like structure, the extension consisting largely of the swollen bases of the successive pairs of protophylls. The stem apex, with the root rather close to it, appears at the end farthest from the foot. Vascular tissue develops between the two apices, so that this region becomes the permanent axis of the plant. An examination of a large number of protocorms in various stages of development brings HOLLOWAY to the conclusion that the organ may be regarded as a physiological specialization to carry the plant over the dry season, and that too much phylogenetic significance should not be attached to it. Such an interpretation would accord, more or less, with BOWER'S "gouty interlude" theory.

The vascular anatomy of the adult plant was studied in 11 species, and in 8 of these the sporeling was also available. In the sporeling there is, at first, a single crescentic group of protoxylem embracing a single group of protophloem; later, the structure becomes diarch, triarch, tetrarch, etc., by the splitting of protoxylem groups, so that the pattern assumes the radial arrangement, the banded condition coming later. In the adult plant, the radial type is found in *L. Selago*, *L. Billardieri*, and *L. varium;* a mixed type in *L. cernuum*, *L. laterale*, and *L. Drummondii;* and a parallel type in *L. volubile*, *L. densum*, *L. fastigiatum*, and *L. scariosum*. The general conclusion is that the various sections of the genus have not been separated from very

ancient times, but that there are rather close interrelationships in which points of contact and divergence may be traced.

The latest paper, issued in July, 1917, deals with methods of vegetative propagation, both gametophytic and sporophytic. In prothallia, vegetative multiplication is accomplished by decay of intermediate parts of elongated specimens and by the isolation of branches in irregular forms. In the sporophyte, methods are more diversified. Bulbils, like those so well known in the *L. Selago* section, are common. In *L. cernuum* bulbils are formed which look exactly like protocorms, except that there is no foot; some of these have as many as 6 protophylls. Reproduction by root tubercles was found in *L. cernuum* and *L. ramulosum*. In the latter species gemmae are produced from cortical cells of the root and even detached leaves may bear bulbils resembling the protocorms of the species. Finally, the elongated protocorms of *L. laterale* and *L. ramulosum* may give rise to new plants by branching and by budding.

HOLLOWAY is continuing his studies and, with abundant material and opportunities for observation, will doubtless give us accounts of the internal structures of prothallia and protocorms and especially the development of the vascular system of the sporeling and its transition to the vascular system of the adult plant.

PSILOTALES.—With the exception of LANG'S description of a single specimen, provisionally referred to *Psilotum*, the gametophytes of the Psilotales have been entirely unknown. It was expected of LAWSON that when he became established in the University of Sydney he would discover these gametophytes and give us an account, since the Psilotales are the only pteridophytes in regard to whose prothallia we have had no information. Two papers[4] have already appeared and another, dealing with the embryogeny, is in preparation. While *Tmesipteris* is epiphytic, notably on tree ferns, LAWSON also found it growing in soil, and it was in such a situation that he found prothallia in greatest abundance. *Psilotum* is more xerophytic, growing in clefts in the rocks, but it also thrives in moist situations, even in the spray of waterfalls, and in these moist places most of the prothallia were found.

In some features the gametophytes of the two genera are very similar. Both are subterranean and tuberous, light brown in color, and uniform in tissue, with no differentiation into vegetative and reproductive regions. An endophytic fungus is found in most of the cells, there being no localized fungal regions. Rhizoids come from all parts of the prothallium. Archegonia and antheridia are borne on the same individual and are not localized, but are scattered over all parts of the plant. The antheridia are spherical and produce a large number of coiled, multiciliate sperms. The archegonium consists of a

[4] LAWSON, A. ANSTRUTHER, The prothallus of *Tmesipteris tannensis*. Trans. Roy. Soc. Edinburgh **51**:785–794. *pls. 1–3*. 1917.

———, The gametophyte generation of the Psilotaceae. Trans. Roy. Soc. Edinburgh **52**:93–113. *pls. 1–5*. 1917.

venter which lies below the surface of the prothallium and a straight neck which projects as a short tube beyond the surface. The organization of the axial row was not worked out in detail. One figure shows an archegonium with an egg and two free nuclei in the neck canal.

In minor features the two genera differ. In *Tmesipteris* the archegonia are much more numerous than the antheridia, while in *Psilotum* the reverse is true. The archegonia and antheridia of *Tmesipteris* are about twice the size of those of *Psilotum*. The statement that the gametophyte generation of the Psilotaceae bears no structural resemblance to the prothallium of *Lycopodium* or *Equisetum* seems peculiar. We readily agree that there is no suggestion of *Equisetum* characteristics, but both the descriptions and the numerous excellent figures constantly remind one of *Lycopodium*, especially of the *L. Phlegmaria* type. LAWSON closes with the remark that no new facts were revealed which would discount the view, now generally held, that the Psilotaceae are more nearly related to the extinct Sphenophyllales than to any other known group of pteridophytes. This may be true, for the prothallia of the Sphenophyllales are entirely unknown and probably will remain so; but if they should be discovered, we should expect them to be of the *Equisetum* type. As far as the evidence of prothallia goes, we should guess that it indicates relationship with the Lycopodiales. The investigation of the embryogeny will be awaited with interest, since it will have a more definite bearing upon the problem of relationships.—CHARLES J. CHAMBERLAIN.

Photosynthesis.—BROWN and HEISE[5] have made a careful study of the experiments of various investigators on the relation of light intensity to photosynthetic rate. They conclude that "the published work on photosynthesis does not warrant the general conclusion that carbon dioxide assimilation in plants is proportional to the light intensity. Instead they indicate a progressively smaller augmentation of the rate of assimilation for each increase in light intensity. This decrease in rate of augmentation continues until a point is reached at which further increase in light produces no measurable increase in assimilation."

BROWN and HEISE[6] have also scrutinized the literature on the effect of temperature on photosynthetic rate and have come to the following surprising conclusions. The temperature coefficients (Q_{10}) lie between 1 and 1.4. They are smaller than those for most vital phenomena which have values agreeing with the Van't Hoff law. These coefficients are of a magnitude that indicates that photosynthesis is a purely photochemical process.

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[5] BROWN, W. H., and HEISE, G. W., The relation between light intensity and carbon dioxide assimilation. Philippine Jour. Sci. **12**:85–95. 1917.

[6] ———, The application of photochemical temperature coefficients to the velocity of carbon dioxide assimilation. Philippine Jour. Sci. **12**:1–24. 1917.

These conclusions are quite out of accord with those of the principal investigators in this field. KANITZ,[7] in his monograph on temperature and life processes, gives the following table, calculated from the experiments of MATTHAEI on the cherry laurel leaf, probably the most nearly error-free piece of work done upon carbon assimilation as effected by temperature.

Temperature	Assimilation CO_2	Q_{10}
−6	0.2	
0	1.75	28.7
10	4.2	2.4
20	8.9	2.12
30	15.9	1.76
37	23.8	1.81
40.5	14.9	0.23

KANITZ points out that the Van't Hoff law applies between 0 and 37° C. He also emphasizes the fact that the coefficient is excessive near the minimum temperature for the process and too small near the maximum, as is true for vital processes generally. The coefficients give no indication that photosynthesis is a purely photochemical process. BAYLISS[8] classifies it as a complex photochemical reaction with increased energy; it results from the combination of purely chemical reactions with photochemical effects. The purely chemical phases seem to be the rate-determining portion, hence the high temperature coefficients. BOVIE[9] gives a similar interpretation of the high temperature coefficients of the process.

The authors misquote KANITZ's formula for calculating Q_{10}. DENNY's review, upon which they depended, misquotes it, due to a typographical error, but they have altered it still further.

NYBERGH attempted to show that photoperception in plants is purely photochemical. His main proof was the small temperature coefficient. DE VRIES has since shown that the coefficient is relatively large and that the process obeys the Van't Hoff law from 10 to 30°C.

It is possible that too much emphasis has been placed upon the size of the temperature coefficient as evidence for the chemical or physical nature of processes in the organism.[10] In the organism, the process often consists of a great number of individual chemical reactions and its rate is the resultant of the rates of all of them. On the other hand, we cannot have too many data on the effect of temperature (or any other factor) on the rate of vital processes or know too much about temperature coefficients which express this effect.–WM. CROCKER.

[7] KANITZ, ARISTIDES, Temperatur und Lebensvorgange. Berlin. 1915.

[8] BAYLISS, W. M., Principles of general physiology (pp. 553–556). London. 1915.

[9] Science N.S. **37**:373–375. 1913.

[10] LEITCH, I., Some experiments on the influence of temperature on the rate of growth in *Pisum sativum*. Ann. Botany **30**:25–46. 1916.

Osmotic concentration and habitat.—The influence of habitat and environmental conditions upon the sap concentration of leaf cells has received considerable attention recently from HARRIS and his co-workers. The cryoscopic method has been used in all determinations of the concentration of tissue fluids, and the studies have now become sufficiently extensive to permit comparisons between the average conditions found in plants of different regions. The mangrove vegetation of Jamaica and Florida[11] has been examined with reference to the influence of salinity of soil water on leaf sap concentration. Three species belonging to three different families were used. The sap concentration is high in all of them, 25–50 atmospheres. *Avicennia nitida* develops the highest concentration of the three, but shows the least variation with environment. *Rhizophora mangle* gave freezing point depressions equivalent to 22–30 atmospheres, and showed distinctly lower leaf sap concentration in fresh water habitats. *Laguncularia racemosa* responded most noticeably, with about 20 atmospheres in fresh water, 25 atmospheres in normal sea water, and 33 atmospheres on sterile mud flats where the sea water is concentrated by evaporation.

A similar study has been made of the Jamaican Blue Mountain rain forest vegetation,[12] where the rainfall averages from 100–130 inches per year. Only terrestrial plants have been reported upon so far, coming from four distinct sub-habitats: the ruinate of leeward slopes, leeward ravines, ridges, and windward slopes and ravines. The plants of each habitat are grouped as ligneous and herbaceous. Distinct differences in the concentration of the tissue fluids of plants growing in each habitat were found, and, as in previous work, the ligneous plants of each type habitat proved to have more concentrated leaf sap than the herbaceous group. The average osmotic concentration of the ligneous plants is about 11.44 atmospheres, and of herbaceous plants 8.8 atmospheres. These figures are lower than for any region thus far investigated, and contrast strongly with values obtained from our southwestern deserts, where herbaceous plants reach 15 atmospheres and ligneous plants 25. In ascending order of sap concentration, the four sub-habitats stand as follows: the windward slopes and ravines, leeward ravines, ridge forests, and ruinate.

Variation in leaf sap concentration with height of insertion on the tree[13] has been studied also, and DIXON'S results confirmed, that the concentration of sap is almost always higher, the higher up the leaf is on the tree. Since, however, the specific electrical conductivity of the sap usually decreases from lower to higher levels, it is probable that photosynthetic sugars are produced

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[11] HARRIS, J. ARTHUR, and LAWRENCE, JOHN V., The osmotic concentration of the sap of the leaves of mangrove trees. Biol. Bull. **32**:202–211. 1917.

[12] ———, The osmotic concentration of the tissue fluids of Jamaican montane rain forest vegetation. Amer. Jour. Bot. **4**:268–298. 1917.

[13] HARRIS, J. ARTHUR, GORTNER, ROSS AIKEN, and LAWRENCE, JOHN V., The relationship between the osmotic concentration of leaf sap and height of leaf insertion in trees. Bull. Torr. Bot. Club **44**:267–286. 1917.

more abundantly in the upper parts of the trees, and are the cause of increased sap concentration. Any agreement between observed increments of osmotic pressure and theoretical values calculated from the increased hydrostatic head and resistance to be overcome in the tracheae by virtue of higher position is regarded as a coincidence, and not as a proof of adjustment on the part of the cells to the back pull of increased head and resistance.—CHARLES A. SHULL.

Antagonism.—Antagonism between iron and manganese in their effects on the growth of two varieties of wheat has been investigated by TOTTINGHAM and BECK.[14] Manganous chloride in water cultures even in low concentrations reduces root growth, but when ferric chloride is added in about equimolecular (0.00001M) concentration the deleterious effects of the manganous salt are overcome. The two varieties of wheat used did not give exactly the same results, and it is believed that effects will depend on variety to a certain extent. Thus the amount of reserve iron in the seed would influence the response of the plant to variations in supply of salts of these two metals. In very dilute solutions the manganous chloride seemed to have stronger effects than ferric chloride on the color and growth, while in higher concentrations (0.001M) the iron salt had more effect than the manganese. Although the concentrations used approach that of these salts in the soil solution, no conclusions as to antagonism in soil cultures can be drawn because of the great variety of other salts and conditions which might modify the result.

SKINNER[15] has studied the effects of manganese sulphate and some other inorganic substances in overcoming the unfavorable action of vanillin and salicylic aldehyde on plants grown in culture solutions of varying composition. He finds that vanillin reduces the growth of cow peas, but the presence of nitrate reduces the unfavorable action, and may even entirely overcome the reduction of growth caused by vanillin. The harmful effects of salicylic aldehyde in 5 and 10 ppm. concentrations on wheat seedlings were entirely overcome by manganese sulphate in 10 ppm. concentration; and the harmfulness of vanillin was also partially overcome by manganese sulphate. He explains the action of nitrate and manganese on the ground that they favor root oxidation, whereby the harmful organic compounds are oxidized and are not permitted to influence growth unfavorably.—CHARLES A. SHULL.

The embryo sac of Aster and Solidago.—These much investigated embryo sacs have been studied again, this time by PALM,[16] a pupil of ROSENBERG.

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[14] TOTTINGHAM, W. E., and BECK, A. J., Antagonism between manganese and iron in the growth of wheat. Plant World **19**:359–370. 1916.

[15] SKINNER, J. J., The effect of vanillin and salicylic aldehyde in culture solution and the action of chemicals in altering their influence. Plant World **19**:371–378. 1916.

[16] PALM, BJ., Zur Embryologie der Gattungen *Aster* und *Solidago*. Acta Horti Bergiani **5**:1–18. *figs. 27*. 1914.

Aster novae-angliae and *Solidago serotina* were the principle species under examination. Several figures show that a tetrad of four megaspores is formed, as would have been expected. In regard to later stages, PALM disagrees with the results of the reviewer[17] and the subsequent study of Miss OPPERMAN,[18] for he claims that the extensive development in the antipodal region is due to the growth of the lower megaspores of the tetrad. His series is far from complete, however, and his figures, interpreted in this way, do not show any antipodal cells. While my own series, published more than 20 years ago, was incomplete, and Miss OPPERMAN'S lacked stages in the early development, I see no reason why either of us should change our view that the chalazal development results from the enlargement of one or more of the antipodal cells. To prove his claim, PALM should present figures of the 8-nucleate stage of the sac, followed by a close series showing the disappearance of the antipodal cells or nuclei. Since such figures are lacking, we prefer to interpret the enlarged cells in the chalazal region as antipodals and not as persistent megaspores.—CHARLES J. CHAMBERLAIN.

The vegetation of Connecticut.—Continuing the studies previously noted,[19] NICHOLS[20] in a fourth paper has considered the vegetation of the swamps and bogs of Connecticut. The latter presents the more interesting group of plant associations, conspicuous among which is the bog forest of *Picea mariana* and *P. rubra*, occasionally supplemented by *Pyrus americana*, constituting a remarkable aggregation of northern trees. These trees, together with shrubs and herbs of northern affinities, lead the author to a consideration of the much discussed question of the origin of bog vegetation, resulting in the opinion that the vegetation is that of a relic swamp type, representing the vestigial remnants of a more northern type of flora which dominated the region within a geological time decidedly more recent than the Pleistocene.

In a similar connection it is interesting to note that in the fifth paper attention is directed to the fact that the rock ravine is second only to the bog for its display of northern species. This paper gives a careful survey of the plant communities associated with stream erosion and deposition. None of the associations are of striking interest, but it serves to round out a comprehensive study of the vegetation of the state.—GEO. D. FULLER.

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[17] CHAMBERLAIN, C. J., The embryo sac of *Aster novae-angliae*. BOT. GAZ. **20**: 205–212. *pls. 15, 16.* 1895.

[18] OPPERMAN, MARIE, A contribution to the life history of *Aster*. BOT. GAZ. **37**:353–362. *pls. 14, 15.* 1914.

[19] BOT. GAZ. **59**:159–160. 1915.

[20] NICHOLS, G. E., The vegetation of Connecticut. IV. Plant societies of the lowlands. V. Plant societies along rivers and streams. Bull. Torr. Bot. Club **42**:169–217. *figs. 15.* 1915; **43**:235–264. *figs. 11.* 1916.

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